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TEMPERATURE DETERMINATION OF SEX IN A PARTHENOGENETIC PARASITE, *OOENCYRTUS SUBMETALLICUS* (HOWARD) (HYMENOPTERA: ENCYRTIDAE)

By F. Wilson* and L. T. Woolcock*

[*Manuscript received December* 29, 1959]

Summary

Ooencyrtus submetallicus, an egg parasite of *Nezara viridula* (L.), reproduces by thelytokous parthenogenesis. The males are functionless. Gynandromorphs occur: these are basically female with male areas of variable extent in the anterior portion of the body. The males and gynandromorphs are usually rare but can be produced at will in considerable numbers under particular conditions.

Development in *O. submetallicus* occurs within a temperature range of 60–90°F. Reproduction is slow at 70°F or lower and rapid at 80°F, whilst temperatures above 85°F cause considerable mortality in the immature stages.

Sex is determined by the temperatures to which a parent female is exposed during development and during adult life. 85°F is the critical sex-determining temperature. Lower temperatures produce female progeny, temperatures of 85°F or higher produce male progeny. Gynandromorphs evidently arise when the parent female, at a critical stage of egg development, is exposed successively to female-producing and male-producing temperatures. The degree of maleness of the gynandromorph is apparently dependent on the stage of egg development at which this change of temperature occurs. Ability to reproduce is retained only by weakly male gynandromorphs.

The sex of the eggs deposited during the first few days of adult life is determined by pre-emergence temperatures: the sex of eggs laid subsequently may be largely determined by post-emergence temperatures. High (male-producing) pre-emergence temperatures appear to have a more profound and persistent effect on sex of the progeny produced subsequently than do low (female-producing) pre-emergence temperatures.

I. INTRODUCTION

Howard (1896) described *Encyrtus submetallicus* from females collected in Granada, British West Indies. The male has not been described. The species, which has since been recorded from the adjacent islands of St. Vincent, Barbados, and Trinidad, is an egg parasite of *Nezara viridula* (L.) (Pentatomidae). Gahan (1927) placed the species in the genus *Ooencyrtus*.

O. submetallicus was imported into Australia for the biological control of *Nezara viridula smaragdula* (F.). A culture, sent by the Commonwealth Institute of Biological Control from Trinidad, has been maintained at the Division of Entomology, C.S.I.R.O., Canberra, since 1952. Specimens sent to the Commonwealth Institute of Entomology were identified by G. J. Kerrich.

The female parasite oviposits in the host egg, within which development to the imago is completed. Several eggs may be deposited in one host, giving rise to

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several adult offspring, but usually, if a female is provided with more hosts than she can parasitize, most eggs yield only one adult.

The great majority of the Hymenoptera reproduce biparentally, but uniparental reproduction has been recorded in species in over 30 genera (Clausen 1940). This uniparental reproduction is usually termed thelytokous parthenogenesis although occasional males have been reared in most species. Reproduction in *O. submetallicus* is by constant thelytokous parthenogenesis, and males are usually rare. This appears to be the first record of this form of reproduction in *Ooencyrtus*. Few biological studies of species of this genus have been made, but two of the best-known species, *O. johnsoni* (Howard) (Maple 1937) and *O. kuvanae* (Howard) (Crossman 1925), are both biparental, exhibiting arrenotokous parthenogenesis.

The male of *O. submetallicus* is apparently functionless. It pursues a female that is moving, and stands before it face to face when it comes to rest, but after several such pursuits it desists until another female appears. Sexual behaviour has evidently degenerated to a stage at which the adults do not proceed to copulation.

The males and females differ greatly in size, colour, and external morphology, and can be readily distinguished by antennal, cephalic, thoracic, or abdominal characters. Individuals occur which consist of mosaics of male and female areas. Hundreds of such individuals (here termed gynandromorphs) have been examined, and the extent of the male and female areas varies greatly. In a series of gynandromorphs arranged in order of increasing maleness, male areas appear first on the head and antennae, and then on the thorax. A weakly male gynandromorph may have a male area only on a small portion of the head or on one antenna; a strongly male individual will have entirely male antennae, head, and thorax. The abdomen is always essentially female, but in strongly male specimens it is smaller and modified in appearance, and the ovipositor may be much reduced in size. The two sexes and gynandromorphs are shown in Plate 1.

Usually only a small proportion of males and gynandromorphs appear in a culture of *O. submetallicus*. For example, the numbers occurring in a culture during 20 months were as follows:

♂ 126; ♀͡♂* 6; ♀ 14,996.

However, a sharp change in sex ratio (exemplified in Table 1) occurred during the summer in several years. The culture was maintained under conditions which suggested that temperature was responsible for the change.

II. Methods

Nezara viridula smaragdula oviposits in masses which usually contain 40–80 eggs. Egg masses obtained within 24 hr of deposition were stored at 4°F. The eggs are killed by this temperature, but they continue to be suitable as hosts while their contents remain liquid, which is usually for 6 months or longer.

Such egg masses were attached by gum tragacanth to cardboard slips, to which droplets of honey were added as food for the adult parasites. Each slip bearing one egg mass was inserted in a 4 by 1 in. glass tube, the opening of which was plugged with cotton wool. One female *O. submetallicus*, initially 0–24 hr old, was placed in each tube for 3 days unless otherwise specified. All tubes were kept in closed boxes containing a saturated solution of potassium chloride, which maintained a relative humidity of about 85 per cent. The boxes were kept in darkness except during periods of observation. The number of hosts in the egg mass was in excess of the number the female could parasitize. Each parent female had emerged from an isolated egg which produced only one parasite, and consequently any possibility that the female had mated was excluded. Successive generations were obtained in the same way by using single virgin females as parents. Unless otherwise stated, the lines were replicated three times and each replicate was maintained separately. The progeny were sexed.

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* The symbol ♀͡♂ is used throughout to designate gynandromorph.

Table 1

CHANGES IN THE SEX RATIO OF ADULTS EMERGING IN A CULTURE OF O. SUBMETALLICUS DURING THE PERIOD JANUARY 10 TO APRIL 16, 1956

Period	No. of Adults of each Sex		
	♂	♀♂	♀
Jan. 10–Feb. 6.	2	2	1016
Feb. 7–Feb. 13.	343	95	88
Feb. 14–Feb. 20	95*	37	1008
Feb. 21–Feb. 27	37*	—	1118
Feb. 28–Mar. 5	10	—	320
Mar. 6–Apr. 16	13	7	1487
Totals	500	141	5037

* Size of culture temporarily increased.

Parasitism of the host by *O. submetallicus* can be recognized from an early stage by two signs—the pedicel of the parasite egg protrudes through the wall of the host, and a dark area develops within a day or two around the point of insertion of the egg.

Part of the adult progeny fails to emerge from its hosts; this is generally small for females but markedly greater for males and gynandromorphs. Counts of the sexes below include all progeny reaching the adult stage, whether or not they succeeded in emerging.

The experiments described were concerned with the sex of progeny reared at different constant temperatures.

III. Experimental Results

(*a*) *Series* 1

Lines, begun with females from a culture kept at 80°F, were maintained at constant temperatures of 60, 70, 80, 82·5, 85, 87·5, 90, and 95°F. The fluctuations at each temperature were almost always within ±1°F. All lines were replicated three times except one that was replicated eight times. Lines which ended because of lack of female progeny were restarted when possible by using females from corresponding replicates. The lines at 85°F were repeated twice. The results are given in Table 2 in which, for brevity, the data of successive generations are combined for lines in which there is no significant difference between generations.

Table 2

SEX OF ADULTS OF O. SUBMETALLICUS IN LINES REARED AT CONSTANT TEMPERATURES (SERIES 1)

Line	Temp. (°F)	Generation	No. of Adults of each Sex*		
			♂	♀♂	♀
A	60	1	—	—	—
B	70	1–8	7	—	110
C	80	1–5	—	—	370
D	82·5	1–5	1	—	328
E	85	1	—	—	57
		2	32	—	—
F	85	1	—	—	47
		2	32	4	1
		3	4	1	—
G	85	1	1	—	158
		2	23	12	10
		3	6	3	5
		4	1	—	2
		5	12	—	—
H	87·5	1	—	—	29
		2	6	—	—
I	90	1	—	—	2
		2	—	—	—
J	95	1	—	—	—

* The number of adults is for 3 replicates per generation in all instances except the following: F, third generation—1 replicate; G, first and second generations—8 replicates, third and fourth generations—4 replicates, fifth generation—1 replicate; I, second generation—1 replicate.

Little oviposition and no evident development took place at 60°F. Reproduction was slow at 70°F and rapid at 80 and 82·5°F; it declined at higher temperatures, and no second generation was produced at 90°F, and no reproduction occurred at 95°F.

The lines at 70, 80, and 82·5°F were deliberately discontinued: the lines at higher temperatures ceased through the absence of female progeny.

First-generation progeny at all temperatures were virtually all female, as were those of subsequent generations at 70, 80, and 82·5°F. At 85°F, only male and gynandromorph progeny appeared within 2–5 generations; at 87·5°F, males only were produced in the second generation.

At lower temperatures (except 60°F) few parasitized eggs failed to produce adult parasites, but at 85°F or higher many progeny failed to develop to maturity. Table 3 gives mortality data for lines reared at 85, 87·5, and 90°F, the data being derived partly from the lines of series 1 and partly from other similar experiments. Most mortality occurred in the earlier developmental stages.

Table 3

MORTALITY IN THE DEVELOPMENTAL STAGES OF O. SUBMETALLICUS REARED AT 85, 87·5, AND 90°F

Temp. (°F)	No. of Host Eggs:				
	Parasitized	Producing Adults	Not Producing Adults		
			Stage of Progeny at Death		
			Egg or Young Larva	Older Larva	Pupa
85	237	57	147	14	19
87·5	193	58	119	11	5
90	174	2	102	63	7

(*b*) *Series* 2

Three lines, begun with females from a culture at 80°F, were maintained at constant temperatures of 84, 85, and 86°F. With rare exceptions, the fluctuations at each temperature were within ±1°F.

The results are given in Table 4, in which the data obtained after the second generation at 84°F are, for conciseness, combined, as there was no significant difference between generations.

The line at 84°F produced predominantly females in all generations, and was discontinued after 11 generations. The lines at 85 and 86°F ceased in the second generation; they produced only females in the first generation and no females in the second generation. It is evident that a temperature of 85°F is critical for sex determination.

(*c*) *Series* 3

A line (five replicates), begun with females obtained from a culture at 80°F, was kept for three generations at alternate daily temperatures of 80 and 85°F. With occasional exceptions, fluctuations were within ±1°F.

In addition, sisters of the parents of the second and third generations were kept under these same conditions but were provided continuously with hosts for virtually the whole of the reproductive period, each female being provided with a fresh egg mass twice each week.

Table 4

SEX OF ADULTS OF O. SUBMETALLICUS IN SUCCESSIVE GENERATIONS OF LINES REARED AT 84, 85, AND 86°F (SERIES 2)

Line	Temp. (°F)	Generation	No. of Adults of each Sex per 3 Replicates		
			♂	♀͡♂	♀
A	84	1	1	—	63
		2	2	1	58
		3–11	16	1	386
B	85	1	—	—	37
		2	27	1	—
C	86	1	—	—	56
		2	20	—	—

The results are given in Table 5. The progeny were nearly all female.

Table 5

SEX OF ADULTS OF O. SUBMETALLICUS REARED AT ALTERNATE DAILY TEMPERATURES OF 80 AND 85°F (SERIES 3)

Period of Reproduction	Generation	No. of Adults of each Sex per 5 Replicates		
		♂	♀͡♂	♀
During first 3 days of adult life	1	2	—	119
	2	—	—	116
	3	—	—	107
During virtually the whole reproductive period	2	1	—	269
	3	2	1	257

(*d*) *Series* 4

This series was reared for three generations at constant temperatures which rarely fluctuated more than ±0·5°F. All progeny were reared at the temperature of oviposition.

The first generation (A) was kept at 80°F, the parent (no replicates) coming from a culture at this temperature. In the second generation, sisters were used as parents (three replicates) at the following temperatures: B and C, 80°F; D and E, 85°F. In the third generation the C and D lines were transferred to 85 and 80°F respectively, whilst B and E continued unchanged. The data obtained are presented in Table 6.

The sex of the progeny depended on the temperature at which the parent was reared, not upon that at which the progeny were reared. Parents reared at 80°F gave rise to female progeny, and parents reared at 85°F gave rise to males and gynandromorphs. Sex in the progeny deposited in the first 3 days of adult life is therefore determined by the temperature to which the parent has been exposed during development. To determine whether this is true for progeny laid after the first 3 days, sisters of the parents of the third generation were kept in comparable experiments under the conditions of B, C, D, and E of the third generation, but were provided with hosts until oviposition ceased, each female being provided with a fresh egg mass twice each week. The results are given in Table 7.

TABLE 6

SEX OF ADULTS OF O. SUBMETALLICUS IN GENERATIONS REARED CONTINUOUSLY OR SUCCESSIVELY AT 80 AND 85°F (SERIES 4)

Parent	Temp.* (°F)	Generation	No. of Adults of each Sex†		
			♂	♀♂	♀
A	80 (80)	1	—	—	22
B	80 (80)	2	—	—	66
	80 (80)	3	—	—	54
C	80 (80)	2	—	—	65
	85 (80)	3	—	—	66
D	85 (80)	2	—	—	65
	80 (85)	3	21	1	—
E	85 (80)	2	—	—	75
	85 (85)	3	37	—	—

* Temperatures given in parenthesis are those at which the parents were reared.

† The number of adults is for 3 replicates per generation in all instances except A, in which there was only 1.

The sex of the progeny continued the same throughout life for B (females) and E (males and gynandromorphs), but tended markedly to change in C (from females to males and gynandromorphs) and D (from males and gynandromorphs to females). Sex of progeny therefore can be determined by the temperatures to which the parent is subjected after emergence.

(*e*) *Series* 5

A line, begun with one female from a culture kept at 80°F, was continued for three generations. The temperatures used were 80 and 87°F, and fluctuations were within ±0·5°F. Progeny were reared at the temperature at which they were laid.

Table 7

SEX OF ADULTS OF O. SUBMETALLICUS FROM SUCCESSIVE EGG MASSES (THIRD GENERATION, SERIES 4)

Parent	Temp.* (°F)	Egg Mass	No. of Adults of each Sex per 3 Replicates		
			♂	♀͡♂	♀
B	80 (80)	1	—	—	97
		2	—	—	50
		3	—	—	23
		4	—	—	3
		5	—	—	7
		6	—	—	—
		7	—	—	—
		8	—	—	1
C	85 (80)	1	—	—	60
		2	3	5	11
		3	3	2	5
		4	4	1	4
		5	2	—	—
D	80 (85)	1	18	—	—
		2	23	8	24
		3	2	—	24
		4	2	—	13
		5	—	—	4
		6	—	—	2
		7	1	—	2
		8	—	—	—
		9	1	—	7
E	85 (85)	1	25	—	—
		2	46	6	—
		2	46	6	—
		3	17	4	—
		4	2	1	—

* Temperatures given in parenthesis are those at which the parents were reared.

The first generation (A) was reared at 80°F. In the second generation, sisters, provided with egg masses (one every 2 days) for the first 20 days of adult life, were kept at 80°F (B) and 87°F (C). In the third generation, sisters from C were allowed to reproduce similarly at 80°F (D) and 87°F (E). The first generation was not replicated: the second and third generations were in triplicate. The results are shown in Table 8.

In A and B the progeny were virtually all female. In C, the first egg masses produced females, and the subsequent egg masses males and gynandromorphs. In D, males were obtained from nearly all egg masses, but females emerged from egg masses 4–8. In E, only a single offspring (male) emerged.

TABLE 8

SEX OF ADULTS OF O. SUBMETALLICUS IN GENERATIONS REARED CONTINUOUSLY AND SUCCESSIVELY AT 80 AND 87°F (SERIES 5)

Generation	1			2						3					
Parent	A			B			C			D			E		
Temp.(°F)*	80 (80)			80 (80)			87 (80)			80 (87)			87 (87)		
Sex	♂	♀♂	♀	♂	♀♂	♀	♂	♀♂	♀	♂	♀♂	♀	♂	♀♂	♀
Egg Mass	No. of Adults†														
1	—	—	30	—	—	35	—	—	34	15	—	—	1	—	—
2				—	—	50	1	1	—	6	—	—	—	—	—
3				—	—	38	3	—	—	2	—	—	—	—	—
4				—	—	31	3	—	—	9	—	7	—	—	—
5				—	—	29	13	3	—	14	—	6	—	—	—
6				1	—	12	—	—	—	9	—	2	—	—	—
7				—	—	8	—	—	—	5	—	3	—	—	—
8				—	—	1	—	—	—	7	—	2	—	—	—
9				—	—	—	—	—	—	3	—	—	—	—	—
10				—	—	—	—	—	—	1	—	—	—	—	—

* Temperatures given in parenthesis are those at which the parents were reared.

† The number of adults is for 3 replicates per egg mass in all instances except the following: A, first egg mass—1 replicate; C, fourth egg mass onwards—2 replicates owing to death of female.

A comparison of series 4 and 5 (Table 9) shows that a temperature of 87°F (whether in the current or preceding generation) produces more males in the progeny than does a temperature of 85°F, and that in the second successive generation at 87°F reproduction virtually ceases.

(*f*) *Series* 6

In this series lines were reared at 80 and 87°F, the fluctuation rarely exceeding ±0·5°F.

The lines were begun with one female derived from a culture maintained at 80°F. The first generation (A) was reared at 80°F. In the second generation, one female (B) was allowed to reproduce at 80°F, and another (C) at 87°F; the progeny were reared at the temperature at which they were laid. The third generation was carried out in triplicate. Sisters from B (D and E) and sisters from C (F and G) were allowed to reproduce for 20 days, each female being provided with an egg mass every 2 days. Exposure to temperature during oviposition was as shown in Table 10. Every egg mass was kept at 80°F from the end of its oviposition period of 2 days. The sexes of the adult progeny of the first two generations were as given in Table 11, and the results obtained in the third generation are set out in Table 12.

TABLE 9

SEX OF ADULTS OF O. SUBMETALLICUS IN GENERATIONS REARED AT 80, 85, AND 87°F (SERIES 4 AND 5)

Group	Temp.* (°F)	No. of Adults of each Sex per 3 Replicates			Temp.* (°F)	No. of Adults of each Sex per 3 Replicates		
		Series 4				Series 5		
		♂	♀♂	♀		♂	♀♂	♀
B	80 (80)	—	—	181	80 (80)	1	—	204
C	85 (80)	12	8	80	87 (80)	20	4	34
D	80 (85)	47	8	76	80 (87)	71	—	20
E	85 (85)	90	11	—	87 (87)	1	—	—

* Temperatures given in parenthesis are those at which the parent females were reared.

TABLE 10

TEMPERATURES DURING OVIPOSITION FOR THE SUCCESSIVE GENERATIONS (SERIES 6)

Oviposition Period (days)	Parents			
	D	E	F	G
	Temperature (°F)			
1–4	80	87	80	87
5–8	87	80	87	80
9–12	80	87	80	87
13–16	87	80	87	80
17–20	80	87	80	87

Parents D produced females until the second egg mass at 87°F, but subsequently nearly all their progeny were male. Parents E (also reared at 80°F) showed a transition in sex of progeny from the second egg mass at 87°F and showed subsequent transitions connected with the changes in temperature. Parents F produced chiefly males, though a few gynandromorphs and females emerged from the fifth egg mass onwards. Parents G produced only males. The numbers of the sexes in the four groups are given in Table 13. Comparing D and E (sisters reared at 80°F), reproduction extended over a longer period in E which produced a far higher proportion of gynandromorphs and males. Comparing F and G (sisters reared at 87°F), F produced more progeny which included some gynandromorphs and females.

The proportions of the sexes and the number of progeny in the above list, and in series 5 (Table 9), support the conclusion that 80°F favoured greater reproduction and female progeny; 87°F caused reduced reproduction and male progeny; while changes in the temperature at which parents were reared and oviposited favoured gynandromorphs. The numbers of eggs in the third generation which were parasitized but failed to produce adults are shown in Table 14.

TABLE 11

SEX OF ADULTS OF O. SUBMETALLICUS IN FIRST TWO GENERATIONS (SERIES 6)

Parent	Generation	Temp. (°F)	No. of Adults of each Sex		
			♂	$\overset{\frown}{♀♂}$	♀
A	1	80	—	—	22
B	2	80	—	—	22
C	2	87	—	—	13

It can be seen from Tables 12 and 14 that the proportion of parasitized eggs which do not produce adults is much higher in oviposition at 87°F than at 80°F.

(*g*) *Series* 7

Gynandromorphs, selected for great variability in degree of maleness, were given the opportunity to reproduce under conditions in which females reproduce readily. Hosts for parasitism were provided in some instances for the first 3 days, in others for the first week, and in others for the whole of adult life. Of 31 gynandromorphs tested, only two gave rise to adult offspring, one producing 12 and the other 21 from 3 days of oviposition. These two gynandromorphs were very weakly male; one showing male coloration near the right mandible, and the other male coloration on a small portion of the head and the metathorax. These individuals, and another which was markedly more male in appearance, also stung a few eggs which did not give rise to adult parasites.

Gynandromorphs live longer than females; 17 gynandromorphs lived for an average of 21 (4–35) days, whilst three females under the same conditions lived for 15 (13–17) days.

TABLE 12

SEX OF ADULTS OF O. SUBMETALLICUS IN THIRD GENERATION, SERIES 6

Oviposition on alternate 2 days at 80 and 87°F; egg masses after 2 days oviposition kept at 80°F

Egg Mass	Oviposition Temp. (°F)	No. of Adults per 3 Replicates						Oviposition Temp. (°F)	No. of Adults per 3 Replicates					
		Parent D (reared at 80°F)			Parent F (reared at 87°F)				Parent E (reared at 80°F)			Parent G (reared at 87°F)		
		♂	♀♂	♀	♂	♀♂	♀		♂	♀♂	♀	♂	♀♂	♀
1	80	—	—	61	2	—	—	87	—	—	33	1	—	—
2		—	—	41	36	—	—		12	7	—	4	—	—
3	87	—	—	34	8*	—	—	80	13	12	3	4	—	—
4		5	1	1	11	—	—		2	6	19	—	—	—
5	80	10	—	—	15	1	—	87	2	1	10	1*	—	—
6		5	—	1	6	1	1		1	—	2	1	—	—
7	87	2	—	1	3	—	—	80	10	2	4	3	—	—
8		—	—	—	2	—	—		3	1	11	3	—	—
9	80	—	—	—	1	—	2	87	1	1	2	1	—	—
10		—	—	—	2	—	—		—	—	—	5	—	—

* Only 2 replicates from this egg mass onwards owing to death of female.

IV. Discussion and Conclusions

Reproduction in *O. submetallicus* occurs within the temperature range of 60–90°F; little or no reproduction occurs at 60 or 90°F; the rate is low at 70°F but high at 80°F (Table 2). At temperatures above 85°F many of the progeny die before reaching the adult stage (Table 3).

At temperatures below 85°F the progeny were almost entirely female, though occasional males or gynandromorphs appeared—possibly as a result of intermittent exposure to higher temperatures during periods of observation. A temperature of 85°F was critical for sex determination (Tables 2 and 4). At 84°F a line consisted almost entirely of females; at 85°F it ceased in 2–5 generations with the production solely of males and gynandromorphs; at 86°F or higher, lines ceased in the second generation which produced only males and gynandromorphs. In lines reared at alternate daily temperatures of 80 and 85°F (Table 5) the progeny were nearly all female.

Table 13

NUMBERS AND SEX OF PROGENY FROM PARENTS D, E, F, G
(THIRD GENERATION, SERIES 6)

Parents	No. of Adults of each Sex			
	♂	♀♂	♀	Total
D	22	1	138	161
E	44	30	84	158
F	86	2	3	91
G	23	—	—	23

Sex of progeny is determined by the temperature to which the parent female is subjected before deposition of the eggs concerned; it is not affected by the temperatures to which the deposited eggs are subjected. This is seen in all the experiments in which lines begun with females reared at 80°F were kept at 85°F or higher, the progeny of the first generation being almost invariably female, and the progeny of the second generation male or gynandromorph (Tables 2, 4, and 6).

The period of parental life in which exposure to temperature determines sex of progeny includes the developmental period before emergence and the oviposition period after emergence. The sex of eggs deposited during the first few days of adult life is determined by the temperature to which the parent is exposed during development: the sex of the subsequent progeny may be largely determined by the temperature experienced by the parent after emergence. This was shown in series 4 (Table 7), where a difference in the temperatures at which parental development and oviposition took place (C and D) is reflected by a change of sex of the progeny. Females deposit many of their eggs in the first few days of adult life, particularly if they have been reared at 80°F (Table 7, B and C), and the temperatures experienced before emergnce are consequently important in determining the sex ratio of progeny.

There is a time lag between the change in temperature to which a female is exposed and the consequent change in the sex of the progeny deposited. This time lag is a measure of the time before deposition that sex is determined. The rapidity of change in sex of progeny consequent on change in the temperature to which the parent is exposed differs according to whether the change is from female-producing to male-producing temperatures or vice versa. This may be seen in series 5 and 6 (Table 8, C and D, and Table 12, D-G). Such differences may, in part, result from the effects of temperature on rate of egg deposition, but it is evident that the data of E and F in Table 12 cannot be explained adequately in this way. It appears rather that high (male-producing) temperatures in the developmental period of the parent produce more profound or persistent effects on the sex of the progeny than do lower (female-producing) temperatures.

TABLE 14

NUMBER OF PARASITIZED EGGS WHICH DID NOT PRODUCE ADULT O. SUBMETALLICUS (THIRD GENERATION, SERIES 6)

Egg Mass	Parent			
	D	E	F	G
	No. of Unproductive Parasitized Hosts per 3 Replicates			
1	3	30	4	5
2	5	36	3	5
3	10	7	8*	—
4	22	3	6	—
5	1	5	—	6*
6	—	7	—	8
7	—	2	—	3
8	—	—	—	—
9	—	2	—	—
10	—	—	2	—
Totals	41	92	23	27

* Only 2 replicates from this egg mass onwards.

It is evident from external morphology that gynandromorphs are basically females with male areas in the anterior part of the body. It is interesting, therefore, that in series 5 (Table 8) some gynandromorphs occurred in C (parents reared at 80°F, progeny at 87°F) but not in D (parents reared at 87°F, progeny at 80°F). Also, in series 6 (Table 12), when parents were exposed to alternating temperatures of 80 and 87°F, E (parents reared at 80°F) produced many gynandromorphs, whilst F (parents reared at 87°F) only produced two after 9–12 days of exposure to temperature alternation. These results indicate that gynandromorphs are individuals exposed initially to a female-producing temperature and then at a critical stage in egg development to a male-producing temperature.

In the third generation in series 4 (Table 7) gynandromorphs appeared in C (second generation at 80°F, third at 85°F), D (second at 85°F, third at 80°F), and E (both at 85°F). Their appearance in C is consistent with the preceding statement; their appearance in D and E may also be consistent with it for, as 85°F is the critical sex-determining temperature, temperature fluctuation (±0·5°F) could allow some individuals to be initially exposed to female-producing temperatures and subsequently to male-producing temperatures. Temperature fluctuation at 87°F would not allow of this result. The marked difference in the numbers of gynandromorphs obtained when temperatures of 85 and 87°F are employed is seen in Table 9.

Nothing is known of the genetics of *O. submetallicus*, though it may be assumed that males are haploid in chromosome number and females diploid, as is the rule in the Hymenoptera. In the absence of cytological evidence, it cannot be asserted that the specimens showing both male and female characters are truly gynandromorphs, that is, that they actually comprise genetically male and female tissues. However, as certain environmental conditions produce females and other conditions produce males, and as transition from the one to the other produces the aberrant individuals, it seems no great assumption that these genetically are combinations of the two sexes produced by the two conditions.

An alternative interpretation is that the "males" are extreme male intersexes, differing phenotypically but not genotypically from the females. If this were so, one would expect the series of intermediates to be complete from the female to the "male". However, the series is complete only from the female to the most male "intersex", after which there is a considerable gap to the "male". Consequently, although the question can be settled only by cytological investigation, it seems likely that we are dealing with true males and gynandromorphs.

It seems very probable that variability in the degree of maleness of gynandromorphs is a function of the point during egg development at which exposure to female-producing temperatures is replaced by exposure to male-producing temperatures; the earlier this change the greater the degree of maleness in the resultant gynandromorph. The ability to reproduce is retained only by gynandromorphs showing slight signs of maleness, that is by those derived from eggs exposed to male-producing temperatures at a relatively late stage of development before deposition.

At high (male-producing) temperatures, mortality in the immature stages is considerable; at low (female-producing) temperatures it is slight. It is not possible, therefore, to explain the occurrence of males and females on the basis of selective mortality of the sexes at different temperatures, nor would such an explanation account for the appearance of gynandromorphs.

Flanders (1945) reviewed the subject of bisexuality in uniparental Hymenoptera and presented evidence supporting the thesis that the sexuality of a uniparental population is an expression of the type of germinal tissues in the preceding generation, the type being determined by environmental conditions. He refers to the following examples of a correlation between male production and temperature in uniparental species:

(1) Speyer (1927) concluded that *Encarsia formosa* Gahan (Eulophidae) produces males only when temperatures are low. Flanders considers that Speyer's data show that the parents of the males developed during a period of high temperature.

(2) Several mymarids of the genera *Anagrus* and *Paranagrus*, bred in Hawaii from January to September, produced males in September only, these being the progeny of females that developed during August, the warmest month of the year.

(3) In the uniparental race of *Diprion polytomum* Hartig (Diprionidae) males are very rare in field populations, but a higher percentage of males were found in warmer regions and, when propagated at temperatures above 70°F, the ratio of males to females was as high as 1 : 37.

(4) In *Habrolepis rouxi* Compere (Encyrtidae) the nature of the host insect and its host plant, as well as temperature, contribute to sex determination. High temperature is necessary to induce arrenotoky.

After reviewing the evidence on the significance of temperature in the production of males, Flanders concludes that developmental temperatures alone do not determine the bisexuality of uniparental populations.

He assembles evidence that in the uniparental species *Microctonus brevicollis* (Halliday) (Braconidae), *Prospaltella perniciosi* Tower (Eulophidae), and the gall-forming *Trichilogaster acaciae-longifoliae* (Frogg.) (Eurytomidae), as well as *Habrolepis rouxi*, male production is correlated with nutrition.

Flanders (1956) has given particular attention to *H. rouxi*; he states that in this species the sex of each offspring is evidently determined nutritionally through the influence of environmental factors on the primordial germ cells of the immature female. Doutt (1959) has reviewed the literature on sex determination in the parasitic Hymenoptera.

The present paper appears to be the first experimental proof for any uniparental species that sex is determined by the temperature to which the parent is exposed. It also appears to be the first demonstration that gynandromorphs can be produced by similar means.

V. ACKNOWLEDGMENTS

The authors wish to acknowledge helpful comments by Professor M. J. D. White, Dr. D. F. Waterhouse, and Mr. G. A. McIntyre, and to thank Mr. G. R. Wearne for technical assistance.

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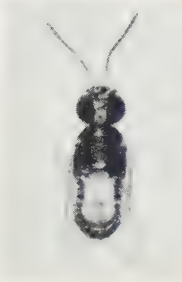
TEMPERATURE AND SEX IN O. SUBMETALLICUS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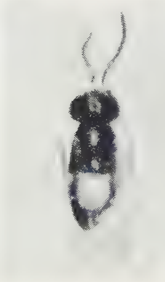
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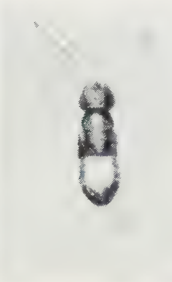
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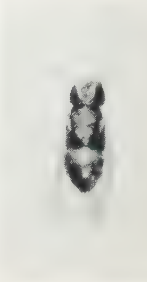
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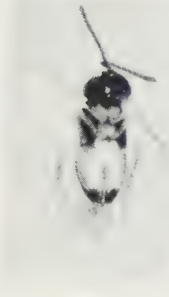
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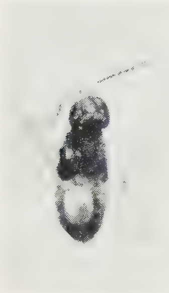
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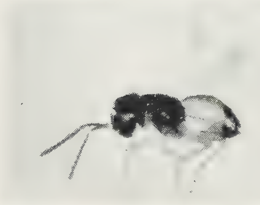
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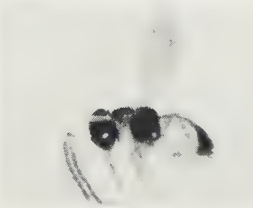
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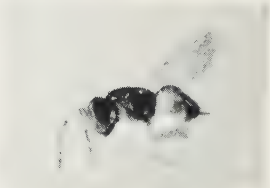
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EXPLANATION OF PLATE 1

The figures show adults of *O. submetallicus*

Fig. 1.—Female, dorsal view.

Fig. 2.—Weakly male gynandromorph, dorsal view. Left antenna and part of head, male; rest of body, female.

Fig. 3.—Strongly male gynandromorph, dorsal view. Antennae, head, and thorax, male: abdomen, female.

Fig. 4.—Male, dorsal view.

Fig. 5.—Female, ventral view.

Fig. 6.—Strongly male gynandromorph, ventral view.

Fig. 7.—Male, ventral view.

Fig. 8.—Female, lateral view.

Fig. 9.—Strongly male gynandromorph, lateral view.

Fig. 10.—Male, lateral view.

THE BIOLOGY OF THE WATER RAT *HYDROMYS CHRYSOGASTER* GEOFFROY (MURIDAE· HYDROMYINAE) IN VICTORIA

By J. McNally*

[*Manuscript received October* 5, 1959]

Summary

In the wild population of water rats studied, males were more numerous and larger than females. In a population of 589 water rats, 323 were males and 266 females. Whole weights ranged from 170 to 1275 g for males and 156 to 992 g for females.

Males were age-grouped into adults (including subadults) and juveniles on the basis of combined testes weights. Sexual maturity is reached when a whole weight of between 400 and 600 g (14–21 oz) is attained.

Females were age-grouped on the stage of maturity of the reproductive tract. Female rats can reproduce when a whole weight of 425 g (15 oz) is attained. Mating takes place in late winter and continues through spring. The breeding season extends from September to January, with the peak in early spring. Females are in anoestrus in late summer, autumn, and early winter. The number in each litter varies from one to seven: the usual number is four or five.

Growth is rapid; young can reach adult size in less than one year. The structure of the population varies throughout the year. The proportion of adults (including subadults) is high in winter and spring and falls in summer and autumn when juveniles appear in numbers.

The fecundity of water rats is lower than normal for murid species, but fertility is high and a substantial population turnover occurs each year when conditions for breeding are favourable. It is considered therefore that the water rat has potentiality for management as an economic fur-bearing animal.

I. Introduction

The water rat, *Hydromys chrysogaster* Geoffroy, 1804, is a native Australian rodent common in Victoria, where it has been protected by law since 1943. Its main habitat is the banks and waters of inland lakes and streams, but it also occurs in estuarine and marine waters.

As a result of protection, and probably also other factors, large populations of water rats exist in the Murray and Goulburn Valley irrigation districts in northern Victoria, where they cause damage to channel banks and to concrete and wooden water-control structures by burrowing through or around them. This results in leakage of water and, in some cases, collapse of the banks or structures.

The cost of maintenance and repairs after such damage is considerable; also the loss of water and occasional flooding of pastures may be important. The State Rivers and Water Supply Commission of Victoria therefore requested that measures should be introduced to control the numbers of water rats in the irrigation districts. Similar requests were made by organizations of irrigators in the areas affected.

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* Fisheries and Wildlife Department, Melbourne.

Water rat pelts are commercially valuable, and compare in quality with those of the American muskrat. Prior to 1943, trappers were permitted to take water rats for pelts under certain conditions. From 1943 to 1958, the water rat was protected throughout the year. An experimental licensed season was proclaimed in 1958 and again in 1959. If the species is found to have potentialities for management as a fur-bearer, the annual removal of the surplus numbers in the populations would provide a method of control which would also utilize the water rat as a natural resource.

An investigation into suitable methods for the conservation and management of the water rat was therefore undertaken by the Victorian Fisheries and Wildlife Department. In order to obtain information on which to base control measures, where these may prove necessary, the extent and nature of the damage was examined, and data on the life history and habits of the water rat were collected. In this paper the biology of *H. chrysogaster* is described, with particular emphasis on its reproduction.

II. Methods

Rats were live-trapped in modified commercial wire cage traps and killed with chloroform or ether to obtain fresh material for examination. Traps were set on the banks of irrigation channels near control structures and on the margins of swamps in the Rochester–Echuca district. Various freshwater and marine fish were used as bait, and rats were caught easily in areas where they were numerous.

Collections were made over the period April 1955 to September 1957. Monthly samples were collected regularly from April 1955 to October 1956. Further samples were taken in February, July, and September 1957 to obtain confirmatory data on reproduction. A complete 12 months sampling programme was carried out in one locality, Murphy's Swamp, near Echuca.

The data obtained from the trapped specimens were recorded on specially printed punched cards. For the majority of the animals examined they included:

(1) Whole and paunched weights.
(2) Body measurements (according to standard Museum practice).
(3) Condition and coloration of pelage.
(4) Diseases, injuries, and parasites.
(5) In males—length and combined weight of testes; presence or absence of motile sperm.
(6) In females—condition of reproductive organs.

The presence of motile sperm was detected by making a smear from an epididymis and examining in a drop of saline solution, under the microscope. Both testes were dissected out, the epididymides and adhering tissue removed, and the two weighed together. The combined weight was recorded. Reproductive tracts were removed from females, placed on strips of paper to retain the shape, and fixed in Bouin's solution for later histological examination. Pelts, skulls, and tibias were collected and preserved.

III. GENERAL BIOLOGY

A description of a typical Victorian specimen of *H. chrysogaster* is given by Brazenor (1936). The species is aquatic in habit. and makes extensive runs and burrows along the margins of the waters where it lives. Although normally found close to water, the rats may move considerable distances overland at night in search of food.

The water rat is mainly carnivorous; its diet includes freshwater fish and molluscs of various species, yabbies, and young aquatic birds and their eggs. Collections of mussel shells and fish and yabbie debris may be found on feeding "tables", or in dens or runs in areas where water rats are present; young mutton birds, *Puffinus tenuirostris* Temminck, and their eggs are taken on the Bass Strait islands. On inland waters the rat attacks fish which have been netted, caged, or tethered by professional fishermen. They also destroy fishing nets and are regarded as a pest. A proportion of vegetable material consisting of coarse grass and rushes is also taken (Brazenor 1936).

Snakes and raptorial birds are predators on water rats. Krefft (1862), refers to the capture of a black snake, *Pseudechis porphyricacus*, which had swallowed 12 young water rats. Calaby (1951) records the observation that 10 ravens, 2 whistling eagles, and a little eagle were observed fighting over the rear portion of a young adult water rat. The species of eagle which originally killed the water rat could not be ascertained.

(*a*) *Injuries and Infections*

The pathology of *H. chrysogaster* was not studied in detail, but obvious symptoms of injury or disease were recorded when observed. Fighting is common amongst water rats and the tails of animals of both sexes were found to be bitten or scarred. Those of older animals were frequently ridged and thickened and exhibited a suppurative condition. This may have been similar to the "curious pathological condition of the tail" observed by Wood Jones (1925, p. 292) on *H. chrysogaster* in South Australia.

Ulcerated wounds and subcutaneous cysts and tumours were noted and some pelts showed a series of punctures on the dorsal surface anterior to the base of the tail. Only one ectoparasite, a flea, was recorded. Four species of helminth parasites were collected. Table 1 gives a summary of the frequency of occurrence of common infections.

Nematodes infested the stomach wall by burrowing into the wall, sometimes in large numbers, and causing a spongy thickening which was visible externally, while the posterior parts of the worms projected into the cavity of the stomach. The species has been identified as *Cosmocephalus australiensis* which is common in South Australian water rats (Johnston and Mawson 1952).

The spargana larvae were found below the skin in the inguinal region and on the shoulders and back. The larvae, which varied in length up to 5 in., were frequently coiled in cysts. When removed and placed in normal saline solution, they showed very slow movements. The genus and species of the adult cestode could be determined by conducting transmission experiments, but this was not done. The cestode which occurred in considerable numbers in the small intestine is probably *Hymenolepis* sp. (a large genus of over 300 species). *Hymenolepis diminuta* Rud., was recorded by Fielding (1927) from *Hydromys chrysogaster* in Queensland. The overall percentage infection in the current investigation was 23 per cent. (147 animals examined). Sample 22 (24 rats) showed a 46 per cent. infection.

Examination of the contents of the alimentary canal and the bile ducts of the liver for the presence of trematodes was not attempted on a large scale as the occurrence of these was of secondary importance to the main investigation. The trematode *Plagiorchis jaenschi* (Johnston and Angel 1951) was recorded from the small intestine of five rats examined. This trematode is stated by Angel to be commonly found in water rats along the Murray R. in South Australia. Johnston and Angel found that the first intermediate host was a mollusc, *Lymnea lessoni*, and the second the yabbie, *Cherax destructor*, although other arthropods could act as hosts. The yabbie is a major food item of water rats.

Table 1

HELMINTH INFESTATIONS OF THE WATER RAT

Type of Infestation	Number Examined	Number Infested	Percentage Infestation
Nematodes in stomach wall	570	268	47
Subcutaneous spargana larvae	456	128	28
Cestodes in small intestine	147	34	23

IV. Sex Ratio and Biometrics

Males outnumbered females—121 males to 100 females (323 to 266 in a total of 589 water rats). In the 21 monthly samples taken, males outnumbered females in 12, females outnumbered males in four, and the sexes were approximately equally represented in five. During the 12-month sampling period on Murphy's Swamp, males outnumbered females in nine samples, females outnumbered males in two, and the sexes were equally represented in one.

It is not clear whether these values indicate a predominance of males in the population, or are the result of biased trapping. Females showed no reluctance to enter traps, even when carrying young. In fact, on occasions litters have been born in traps, so that females were moving about up to the time of delivery.

The biometrics of the water rat, compiled from examination of 433 animals (230 males and 203 females), are shown in Table 2. Whole weights and paunched weights were recorded for only 327 animals (170 males and 157 females).

The whole weights of water rats have been grouped by intervals of 85 g (3 oz) into 14 classes, and frequency distribution histograms have been constructed for 323 males and 266 females. These are shown in Figure 1. The ranges of whole weights are 170–1275 g in males and 156–992 g in females. The modal classes for males were 7 and 8 (631–800 g, 102 individuals); and the modal class for females was 6 (546–620 g, 54 individuals).

TABLE 2

BIOMETRICS OF THE EASTERN WATER RAT

	Males		Females	
	Average	Maximum	Average	Maximum
Whole weight (g)	775	1275	621	992
Whole weight (oz)	27	45	22	35
Paunched weight (g)	680	1134*	557	907
Paunched weight (oz)	24	40	20	32
Total length (cm)	59·0	68·5	56·7	64·0
Head and body length (cm)	31·4	36·5	29·4	34·8
Tail length (cm)	27·6	32·5	27·3	32·0
Ear length (cm)	1·8	2·0	1·8	2·1
Pes length (cm)	7·0	7·8	6·7	7·4

* The maximum paunched weight of 1134 g is that of the second largest animal, a male with a whole weight of 1247 g. The paunched weight of the largest specimen examined was unfortunately not recorded.

V. REPRODUCTION

During the years prior to 1943, when water rats were being trapped for skins in Victoria casual observations were made by trappers in the course of their work. They claimed that, when food and water were abundant, the rats produced several litters in a year, while in dry years breeding was irregular and litters were smaller. That males and females segregate after the birth of the young was suggested by the fact that catches were mainly male or mainly female according to location.

Troughton (1941) states that water rats in Victoria begin breeding in the spring and that the young are not fully developed until the following April. He gives the normal annual litter numbers as four or five. Brazenor (1936) gives four and Lewis (1941) gives three to five, and states that seven have been noted occasionally. Fleay (1949) states that the maximum litter size is four, but usually fewer, and varies from two to four a litter produced in the spring and summer months. He mentions that young rats are seen in the streams in autumn. Fleay also showed that, when the first litter is removed from a female water rat which had reproduced in captivity, a second litter was born 2 months later in the same season.

When the control or management of a species like the water rat, which is probably short-lived, is being considered it is important to be able to identify the young of the year and distinguish them from the adult or subadult animals of the previous breeding seasons. Special attention was therefore given to this problem.

(a) *Maturity in the Male*

For the determination of age and maturity in male water rats, the criteria considered included head and body length, weight, length of tibia, zygomatic and incisor widths, and the state of development of the testes. All but the last were found to be unsatisfactory.

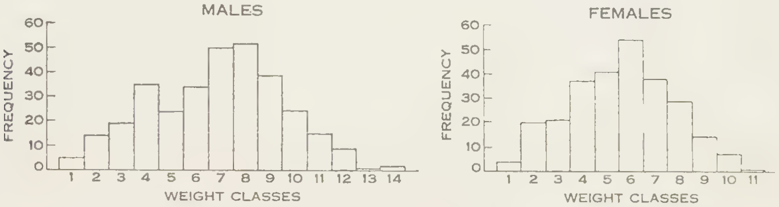

Fig. 1.—Distribution of the whole weights of 589 water rats (323 males and 266 females) by classes of 85 g difference in a weight range of 156–1275 g.

Figure 2, a scatter diagram of whole weights and combined testes weights of 236 rats, shows that, with one exception, all testes lacking motile sperm weighed less than 5 g and were from animals weighing less than 800 g. (The majority of animals without motile sperm weighed less than 600 g.) Rats with combined testes weights of less than 5 g can therefore be classified as juveniles, with very little risk of error; while those with combined testes weights of 5 g and over will be subadult or adults.

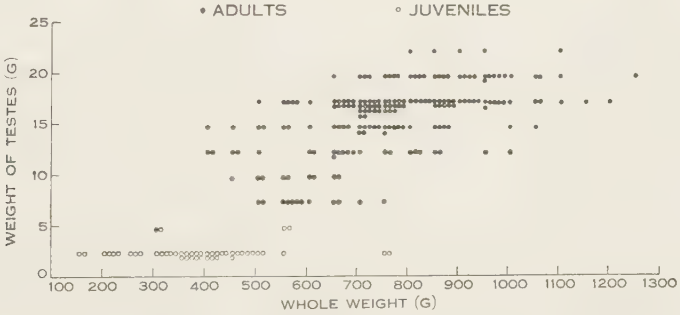

Fig. 2.—Scatter diagram of the whole weights and testes weights of 236 male water rats to show the relationship between the two.

It is clear that weight alone does not provide a satisfactory criterion of age and maturity, as the weight ranges of adults and juveniles show considerable overlap, so that it is possible for a well-developed juvenile to be indistinguishable in size from an adult. Male water rats appear to develop sexual maturity when they attain the whole weight of between 400 and 600 g (14–21 oz).

For the interpretation of population data, it would have been a distinct advantage to be able to distinguish between adult and subadult animals. It is clear from Figure 2, however, that this separation would have to be quite arbitrary.

A small number of marked water rats were kept in captivity at the Melbourne Zoological Gardens during part of 1955–56, to obtain growth-rate data. The amount of information obtained was limited owing to escapes, but it was sufficient to show that growth is extremely rapid in the first 8 months. At 8 months the testes are still in an early stage of development; and it is therefore considered unlikely that males, with the possible exception of those born very early in the breeding season, would reach sexual maturity in the first year of life.

The highest combined testes weights (maximum 21 g) were recorded during spring and summer. Motile spermatozoa were found in male water rats throughout the year, but there was some indication of regression in testes weight in autumn and winter.

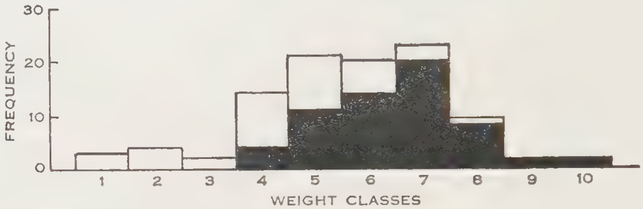

Fig. 3.—Distribution of the paunched weights of 100 female water rats taken during the period September 1, 1955, to January 31, 1956. The weights are in classes of 85 g difference in a weight range of 170–907 g. The shaded area represents reproductive females.

(b) *Maturity in the Female*

Reproductive tracts of female rats were examined *in situ* for stages of development. The condition of the uterine horns was recorded as an indicator of maturity. In juveniles, the uterine horns are thin-walled, in mature animals in the anoestrous phase they are more robust, and in reproductive females they become distended and turgid.

During the breeding period, pregnancies were determined by visual examination of the uteri without sectioning. Where a series of swellings were obvious, showing the number and position of the embryos, a positive pregnancy was recorded. Rats not obviously pregnant were recorded as juvenile or non-reproductive according to body size and stage of development of uterine horns. Pregnant rats with early implantations would not have been detected. Post-partum rats were identified by the presence of placental scars on the uterine horns. These were dark and distinct where the rat had reproduced recently, but faded where some time had elapsed since the young had been born. Some animals showed two sets of scars of different ages, indicating that they were multiparous.

The minimum (paunched) weight recorded for a pregnant female was 425 g (15 oz); and all females under this weight were classified as juveniles. It was not possible to make any distinction between adults and subadults. Figure 3 shows the distribution of the weights of 100 females taken during the period September

1, 1955, to January 31, 1956; of these 61 per cent. were reproductive, 28 per cent. were barren, and 11 per cent. were juvenile.

The age at which females become sexually mature and competent to reproduce could not be determined from the data. However, it is quite possible for a rat to attain a weight of 425 g in the first year of its growth. Whether it would be capable of reproducing in the breeding season following that of its birth would depend on the time of the year at which it was born. It seems probable that the majority of females would not breed until they are more than one year old.

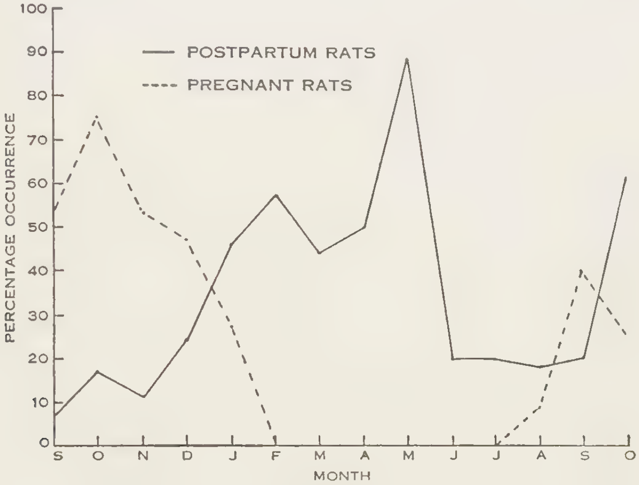

Fig. 4.—Variation in the percentage occurrence of pregnant and post-partum adult female water rats over a 12-month period.

(c) *Breeding Season*

The first positive pregnancies were recorded in early September 1955, when 53 per cent. of females in the monthly sample were pregnant. In October, 75 per cent. were pregnant and 17 per cent. post-partum. The reproductive activity continued through the months of November, December, and January, with decreasing intensity, until no pregnancies were recorded in February 1956. As the incidence of pregnancies decreased that of post-parta increased. Sampling in 1956 and 1957 confirmed that positive pregnancies appear first in any numbers in early September, although one pregnant female was taken in August 1956. There are no data on which an estimate of the gestation period can be based. It would be necessary to determine this from observations on captive animals. The occurrence of pregnant and post-partum females by months over a 12-month period is shown graphically in Figure 4.

These observations indicate that mating takes place in late winter and continues through the spring and early summer. The peak of the reproductive season appears to be in early spring, and the season extends from September to January, a period of 5 months. During the late summer, autumn, and early winter the female rats are in anoestrus.

Changes in the age structure of the water rat population, resulting from the increased contribution of young animals over the summer months, is shown in Figure 5 which traces the monthly variation in the percentages of adults and juveniles in each sample over a 15-month period covering the whole of the 1955–56 breeding season.

(d) *Fertility and Fecundity in Females*

H. chrysogaster has only four mammae with nipples situated in the abdomino-inguinal region. These are small and inconspicuous in non-breeding animals, but some or all are stretched and prominent in reproductive animals during the breeding period. The breeding rate is low compared with other murid species. The majority of females produce litters of four or five. The maximum number of embryos recorded in one rat was six and the minimum one. Examination of placental scars in post-partum rats showed a similar condition. Three animals in 32 showed seven scars, the probable maximum for one litter.

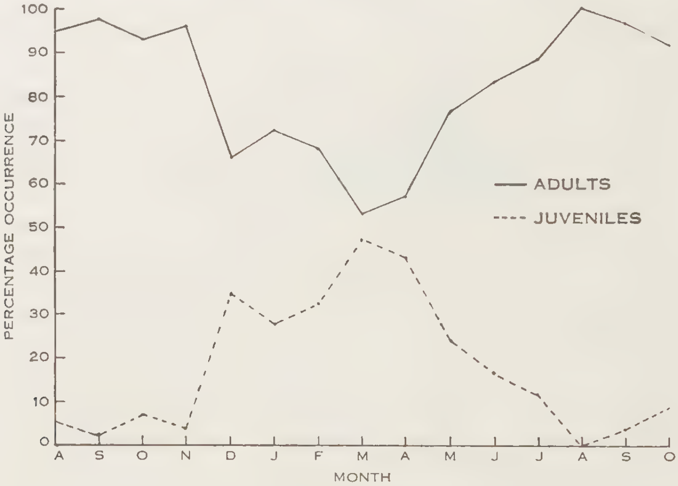

Fig. 5.—Variation by months in the percentage occurrence of adult (including subadult) and juvenile water rats over 15 months, including the whole 1955–56 breeding season.

In view of the fact that only four nipples are available to feed the young, it is probable that the surplus young over and above four, which occur in large litters, would have reduced chances of survival.

Rats in various stages of pregnancy from early implantations, producing only slight uterine swellings, to full term were examined. These showed that implantation may take place either in the right or left uterine horn, or in both simultaneously. 21 females out of 50 carrying four embryos contained two in each uterus. Implantation and the distribution of the embryos between the two horns of the uterus thus seems to be a matter of chance.

Examination of placental scars indicates that one litter per season is normal. However, where more than seven scars were noted, it could be assumed that they were the result of two separate pregnancies. Sometimes, the scars were easily separated into groups on distinctness of coloration, but at other times they were so faint as to be just discernible. Since the time taken for scars to disappear is not known, it cannot be stated with certainty whether two pregnancies occurred in one season, or in two successive seasons.

VI. Discussion and Conclusions

Observations made in the irrigation districts in northern Victoria indicated that the water rat is a serious cause of damage. In some cases they are a secondary cause, the initial damage being the result of burrowing by rabbits or yabbies. It is considered that local control of water rats is warranted in irrigation districts and that a periodical licensed season is the most expeditious means of achieving this control.

A licensed season provides adequate safeguards to ensure that the water rat populations are maintained at a sound level so they can continue to exist without being in sufficiently large numbers to cause serious economic damage. The surplus numbers taken during the seasons provide an economic return from marketing of skins.

It has been shown in this study that there is a substantial annual turnover in the water rat population, providing a surplus available for exploitation without prejudicing the continued existence of the species. It is therefore considered that the water rat has definite potentialities for management as an economic fur-bearer.

The data that have been obtained also show, however, that the fecundity of *H. chrysogaster* is lower than that of most murid species, and lower than that of the muskrat, *Ondatra zibethica*, in which litters of three to eight are normal (average six) and litter sizes vary from one to 13 according to race. If the trapping of water rats for their pelts and to reduce damage to irrigation works is permitted, therefore, the status of the species in the areas where the operations are carried out may need to be carefully watched.

VII. Acknowledgments

The author sincerely thanks Mr. F. N. Ratcliffe and Mr. J. Calaby, Wildlife Survey Section, C.S.I.R.O., Canberra, for criticism of the manuscript and helpful advice; also Mrs. Patricia M. Thomas and Miss L. Madeline Angel, University of Adelaide, and Dr. J. C. Pearson, Veterinary School, University of Queensland, for help with identification of parasites.

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THE INTERNAL ANATOMY OF *TYPHLOPS* SCHNEIDER (REPTILIA)

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Summary

The internal anatomy of *Typhlops* shows a number of interesting features which support the hypothesis that the typhlopids are wrongly classified among the Ophidia, and that they should either be given subordinal rank, equivalent to the Sauria and the Serpentes, or be made an infra-order of the Sauria.

The alimentary, vascular, respiratory, and reproductive systems are described in detail for the first time.

The most striking peculiarities occur in the respiratory and reproductive systems. Unlike most snakes, *Typhlops* has two functional lungs, one occupying most of the anterior third of the body cavity, and the other smaller one lying immediately behind it. All the pulmonary blood vessels are well developed.

The male reproductive organs are solid, grooved, protrusible structures, each of which is contained within a connective tissue sheath in the postanal region. These organs are unlike the hemipenes of any snake or lizard of which a description can be found. Both male and female animals possess a large cloacal gland in the postanal region.

There are also several uncommon features in the alimentary and vascular systems.

I. INTRODUCTION

Although the genus *Typhlops* has been established for over 150 years, comparatively little work has been done on the internal anatomy of the members of this group. Certain aspects of the structure of *Typhlops*, which have taxonomic and phylogenetic significance, have been explored by some workers; for example, Duerden and Essex (1923) and Essex (1927) have made extensive studies of the pelvic girdle of *Typhlops*; Dunn and Tihen (1944) and Tihen (1945) have worked on the osteology of the genus, and Kashyap (1949) has described the heart of *Typhlops*. In addition, Waite (1918, 1929) has written general accounts of the Australian species of blind snakes, but has confined his attention mainly to external features, and to a few aspects of the osteology of the skull.

The present study was undertaken in an endeavour to increase the knowledge of the soft parts of the animal, and, at the same time, to see if such knowledge would throw any light on the phylogeny of the group.

The typhlopids have always been classified among the less specialized of snakes; Boulenger (1893–96) presented a phylogenetic classification of the Ophidia in which he placed the families Typhlopidae, Glauconiidae, and Boidae as the most primitive members of the group. Gadow (1901) described the family Typhlopidae as "undoubtedly the last living descendants of formerly cosmopolitan, rather archaic, snakes, which in adaptation to their burrowing life and insectivorous diet

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have undergone degradation". Lydekker (1912) in writing of the four families of burrowing snakes (the Typhlopidae, Glauconiidae, Ilysiidae, and Uropeltidae) says, "The various burrowing snakes are evidently degraded types which took to a burrowing mode of life at an early stage of the evolution of the Ophidia". Bellairs and Underwood (1951), in discussing the interrelationships of living snakes, comment, "The Leptotyphlopidae and Typhlopidae, while possessing many primitive characters and still remaining in the fossorial stage of evolution, have deviated considerably from the main line of ophidian descent. It is likely that these aberrant families have been derived independently from very ancient ophidian types. Although Makendra regards these two groups as being allied, it would appear from the work of Haas on the skull and jaw muscles that they are not closely related, and it is likely that the superficial resemblance between them is the result of parallel evolution."

Thus uncertainty has grown regarding the exact phylogenetic position of the Typhlopidae, and the family has been pushed more and more to the side of the main ophidian line of descent.

McDowell and Bogert (1954) made a detailed study of the lizards belonging to the genus *Lanthanotus*, based mainly on the external features and the structure of the skull and tongue, and they compared the genus with other members of the superfamily Platynota.

They show that *Lanthanotus* has many of the features to be expected in an ancestor of the snakes, and they suggest that the snakes may have originated from aigialosaurian stock, morphologically similar to the living *Lanthanotus*. They then point out that if the aigialosaurian ancestry of snakes is accepted, it would appear that the Typhlopidae are wrongly placed in the Ophidia, for they show no particular resemblance in cranial structure to either the platynotan lizards or the snakes.

McDowell and Bogert suggest that the Typhlopidae represent a line of anguinid-like lizards that has become convergent to the snakes. They state, "It is equally clear that the many peculiar specializations of the typhlopids (particularly the unique lower jaw mechanism) warrant their separation from the Diploglossa, and, indeed, from the Anguinomorpha". They suggest that the typhlopids should either be given subordinal rank, i.e. equivalent to the Sauria and the Serpentes, or that they should perhaps be an infra-order of the Sauria, i.e. equivalent to the Anguinomorpha.

As will be seen in the following account, the numerous peculiarities of the internal organs of *Typhlops* support the hypothesis that the group should indeed be removed from the Ophidia. The most striking peculiarities occur in the reproductive and respiratory systems, though the alimentary and vascular systems also show several uncommon features.

The following account of the alimentary, vascular, respiratory, and reproductive systems is based on dissections of *T. polygrammicus* (5 specimens), *T. ligatus* (1 specimen), *T. australis* (4 specimens), and *T. proximus* (1 specimen).

II. The Alimentary Canal

There is very little change in the diameter of the alimentary canal of *Typhlops* throughout its length. It is mainly a straight tube, though there is some slight convolution in the intestinal region.

Externally, it is difficult to distinguish the limits of the various regions of the canal; in fact, the pyloric constriction is the only "landmark" of which one can be quite certain. Internally, however, most of the regions are distinctly marked off from each other by very obvious changes in the mucous membrane.

The oesophagus, which lies in the left dorsolateral aspect of the body cavity, extends for approximately half the length of the gut. It is thin-walled, soft, and strap-like, slightly wider at the anterior end than at the posterior end. The longitudinal folds on its internal surface are visible externally.

Towards its posterior limit the wall of the oesophagus becomes gradually firmer and more opaque, making the identification of the junction of the oesophagus and stomach very difficult, though internally the junction is obvious to the naked eye.

The stomach consists of two regions, the anterior cardiac region and the posterior pyloric region. There is some slight external variation between the two, though again the exact line of demarcation is not obvious. The cardiac region is somewhat wider than the pyloric region, and the wall of the latter is very muscular. In one specimen of *T. polygrammicus* dissected, there was a sudden constriction and a slight twist in the gut between the two stomach regions; in other specimens, however, both of this and other species, the change in diameter between the cardiac and pyloric regions was very gradual.

The position of the pyloric sphincter is marked by a very deep, but very narrow, constriction. Immediately behind this the alimentary canal expands suddenly and the bile duct and the pancreatic duct enter the intestine on the ventral shoulder of this distension. From here on for some distance the gut is usually thrown into some degree of convolution, though at no stage could it be described as "coiled".

Towards the end of the small intestine the convolutions diminish, though they do not disappear entirely until a short distance in front of the rectum. Again, the dividing line between the small intestine and the colon is not visible externally—nor, for that matter, is it very clear internally. The colon is very short, and slightly distended. From this region an elongate caecum arises and lies close against the gut, projecting forwards in the body cavity. This structure is soft-walled and is usually darker in colour than the adjacent intestine.

The alimentary canal ends in a very short, very distended rectum, which has a thin membranous wall, and which opens into the cloaca.

Table 1 gives the lengths of the various regions of the alimentary canal of a specimen of *T. polygrammicus*, which measured 365 mm from head to tail.

Internally, and histologically, the alimentary canal shows a much greater degree of differentiation between the various regions than is discernable externally.

The ventrally placed mouth opens into the buccal cavity. The teeth are few in number, and very tiny; they are present only on the upper jaw, attached to the maxilla.

In the dorsal region of the buccal cavity, hidden by the palatal folds, are the very small, paired openings of the vomeronasal organs. Slightly posterior to these are the choanae, from the outer edges of which the palatal folds pass backwards towards the pharynx, thus forming a deep channel for the passage of air. Behind the choanae the roof of the mouth becomes quite steeply vaulted. There are no eustachian recesses.

The tongue is long and thin and very flexible and is deeply forked at its free end; the groove between the two portions extends to the point where the tongue joins its sheath.

TABLE 1

COMPARATIVE LENGTHS OF REGIONS OF THE ALIMENTARY CANAL OF A SPECIMEN OF TYPHLOPS POLYGRAMMICUS

	Length (mm)	Length Expressed as Percentage of Total Length of Gut	
Oesophagus	200	50·5	
Cardiac stomach	20	5·5	8·7
Pyloric stomach	13	3·2	
Intestine	135	34·1	
Colon	15	3·7	
Rectum	12	3·0	
Total length of gut	395		

A little behind the tongue is the median larynx, forming a slight prominence on the floor of the mouth. The glottis is centrally placed on the surface of this prominence and its edges are supported by two closely opposed cartilages.

The oesophagus opens posteriorly from the buccal cavity. Its wall is thrown into a series of very long folds, which mainly extend throughout the length of the organ. Between these longitudinal folds the wall of the oesophagus is very thin and relatively transparent for the great part of its length, but thickens somewhat towards the region of the stomach (Plate 1, Fig. 1).

Histologically, the wall of the oesophagus is very simple, especially in the anterior region. Here the mucosa is composed of columnar cells, the vast majority of which are mucus-secreting. The submucosa is only developed to any appreciable extent in the cavities of the folds of the lining membrane, and muscle tissue is practically non-existent, except for a few, small, scattered areas of longitudinal fibres.

More posteriorly the oesophageal wall shows a greater degree of complexity. The lining columnar epithelium is still largely composed of mucus-secreting cells, and the submucosa is slightly more vascular than in the anterior oesophageal region. The muscle layer is in evidence, though not to any great extent. Circular and longitudinal fibres are present, in two separate bands, which are of approximately equal thickness.

The junction of the oesophagus and stomach is clearly seen internally as a slightly irregular line formed by the ending of the oesophageal folds and the beginning of the maze-like folding of the mucous membrane lining the cardiac region of the stomach (Plate 1, Fig. 2). These folds are very deep, irregular, and branched, and enormously increase the surface area of the lining of this part of the gut.

The mucosa here lacks mucus-secreting cells, but numerous gastric glands are developed as pits in the columnar epithelium. The cells which form the glands are spherical, with granular cytoplasm and large round nuclei. There is a very narrow muscularis mucosa, which extends into the cavities of the folds in the mucosa. The submucosa is a narrow zone, but a very vascular one. The muscle tissue has undergone some change, the band of circular fibres being now somewhat discontinuous, and the band of longitudinal fibres, while remaining continuous, is much narrower than it is in the oesophageal wall.

The cardiac region of the stomach is followed by the pyloric region, a rather tube-like structure, where the lining is again thrown into deep longitudinal folds, which are not straight, as in the oesophagus, but somewhat spiral. The junction between the two regions of the stomach is not sharply marked internally, but over a short area the irregular folds of the cardiac region become straightened out and continue as the longitudinal folds of the pyloric region.

The gastric glands in the pyloric region are smaller and more scattered than they are in the cardiac region. A wide muscularis mucosa is present in the pyloric stomach, and here also the band of circular muscle fibres is enormously developed.

The pyloric sphincter is well developed, and leaves only a very narrow aperture between the stomach and intestine, which can obviously be very tightly closed. The pylorus is a relatively wide, ridged band of muscle tissue, forming a ledge which projects into both the stomach and the intestine.

Immediately behind the pylorus the gut widens considerably, and the lining is thrown up into a dense mass of villi, which are flattened and triangular. The bile and pancreatic ducts open into this region of the gut, and there is an area free of villi in the immediate vicinity of this aperture.

There are no obvious glands in the intestinal mucosa, and the villi are lined with very narrow columnar cells. The muscularis mucosa is not evident. The submucosa is well developed and still very vascular, while the band of circular muscle fibres has decreased greatly in width. Longitudinal fibres are present in a continuous band outside the circular fibres.

This type of lining of the gut wall extends back throughout the greater part of the small intestine; the villi begin to thin out gradually as the colon is approached, and at a point that is very hard to define specifically, the lining becomes ridged once again, and continues thus to the rectum (Plate 2, Fig. 1). The duodenum is only distinguishable by the point of entry of the bile and pancreatic ducts.

The junction of the small intestine and the colon is assumed to be indicated by the point of origin of the elongate caecum (Plate 2, Fig. 2).

In *Typhlops*, the caecum is histologically similar to the region of the gut from which it arises, and in all the animals dissected was filled with food material. The blood supply to the caecum is copious, and comes from the first and second inferior mesenteric arteries. The aperture leading from the intestine into the caecum is situated in the left lateral wall of the gut and is partially overhung by a backwardly directed, semicircular flap of tissue.

In the region immediately posterior to the origin of the caecum, the wall of the gut becomes thinner, mainly due to a decrease in the width of the submucosa.

The alimentary canal ends in a short wide rectum, which opens into the cloaca. For the most part the wall of the rectum is thin, smooth, and membranous, but immediately prior to entering the cloaca, it becomes weakly ridged.

The Liver, Gall Bladder, Pancreas, and Spleen

The liver is a very elongate organ. Its anterior end is just above the tip of the ventricle, and it extends almost into the posterior third of the body. It lies on the right side of the body cavity, and occupies more than half of the width of it. It is red-brown in colour, and firm to touch.

The liver is many lobed, each lobe resembling a short, subcylindrical block, often deeply indented. The anterior and posterior ends of the organ are drawn out into quite pronounced points, both of which are split by a deep groove. Bronn (1883) comments that the lobular nature of the liver in snakes is negligible except in *Typhlops*, where it is distinct.

The postcaval vein is set in a groove along the ventral surface of the liver; it sometimes disappears from sight while passing from one lobe to another, but is clearly visible along the greater part of the ventral surface of each section.

The hepatic portal vein follows an equally conspicuous, but more direct, course along the dorsal surface of the liver, giving many branches into the tissue as it does so.

The hepatic duct gradually forms on the dorsal surface of the liver by the confluence of many small ducts, and on leaving the dorsal surface of the liver at its posterior end, passes backwards in the body cavity in association with the hepatic portal vein and the postcaval vein. It continues to a point a few centimetres past the posterior end of the gall bladder, where it unites with the cystic duct.

The cystic duct arises from the gall bladder at a point approximately one-third of its length from the posterior end, and passes straight back to its point of junction with the hepatic duct.

The common bile duct, resulting from the union of the hepatic and cystic ducts, makes an almost right-angled bend just behind its point of origin, and enters the intestine on the ventral wall, a very short distance posterior to the pyloric valve (Plate 1, Fig. 2).

As the gall bladder is situated some distance behind the posterior tip of the liver, the hepatic duct is a relatively long structure. At its posterior end, the gall bladder, the cystic duct, and common bile duct are all very closely bound together, with the ducts lying between the gall bladder and the pancreas and spleen (Plate 1, Fig. 2). All these structures receive a copious blood supply from the lieno-gastric artery, and are drained by tributaries of the hepatic portal vein.

The gall bladder is oval and globular and is bound to the pancreas and spleen; these three structures lie across the ventral wall of the intestine in the region of the pyloric constriction and therefore obscure the latter.

The pancreas lies on the right of the gall bladder, closely bound to it. It is a white compact organ divided into two lobes lying side by side. It is approximately half the size of the gall bladder.

One short duct leaves each lobe; these two ducts join on the surface of the intestine, and enter its wall immediately alongside the common bile duct.

The spleen is pale cream in colour, only very slightly darker than the pancreas. It is an oval structure, immediately anterior to the pancreas, and very closely bound to it. The posterior end of the spleen is wedge-shaped, and fits between the two lobes of the pancreas.

III. The Blood Vascular System

(*a*) *The Heart* (Figs. 1–4)

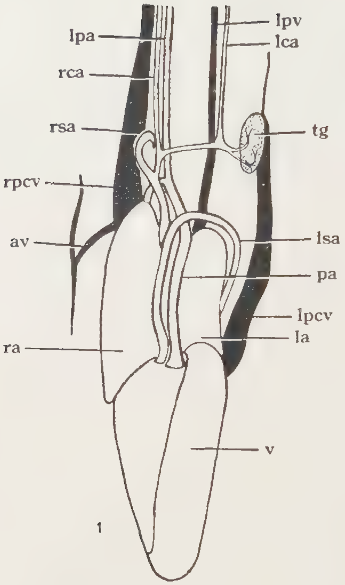
The heart lies in the mid-ventral line of the body cavity, not quite one-third of the body length from the head, and with the tip of the ventricle directed very slightly towards the right. Kashyap (1949) describes the heart of *Typhlops* as being "slightly directed to the left"—but this was not the case in the specimens dissected in the present work.

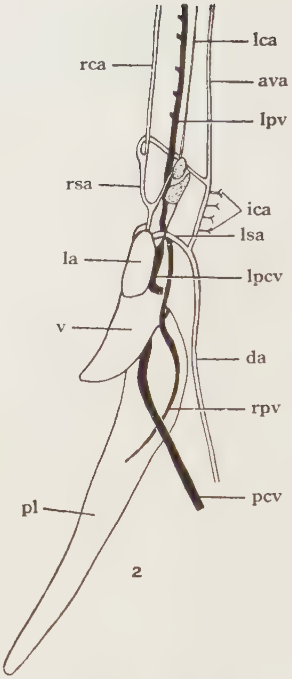
The heart is an elongate organ, cylindrical for the greater part of its length, but tapering somewhat at the posterior tip. It is invested by a delicate pericardium, which is quite free. Beddard (1904) describes a vestigial gubernaculum cordis connecting the pericardium to the heart in several species of snakes, but no trace of such a structure was found in the specimens of *Typhlops* dissected.

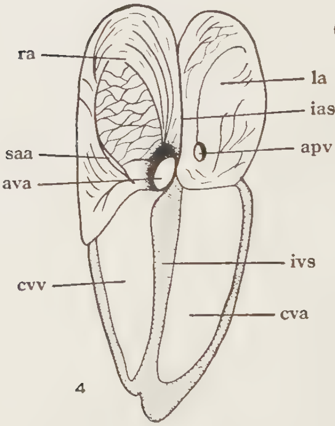
The heart is made up of the following regions: (i) the sinus venosus; (ii) the auricles; (iii) the ventricle.

(i) *The Sinus Venosus.*—The thin-walled sinus venosus is situated on the dorsolateral surface of the right auricle, towards its posterior limit. It is not easy to distinguish the sinus venosus externally as a separate structure, but, since it is formed by the confluence of the bases of the two precaval veins and the postcaval vein, its position can be determined by locating the junction of these vessels with the heart. The right precaval vein and the postcaval vein meet in an almost straight line on the dorsolateral border of the right auricle, while the left precaval vein passes down the dorsolateral aspect of the left auricle, then turns at right angles to follow the coronary sulcus to the point where it finally enters the sinus venosus at its posterior mesial corner (Fig. 3).

The opening of the left precaval into the sinus venosus is an obliquely placed ellipsoidal slit. The opening is guarded ventrally by a valvular flap from the dorsal wall of the right auricle, and dorsally by a ridge on the inside of the dorsal wall of the base of the left precaval vein.







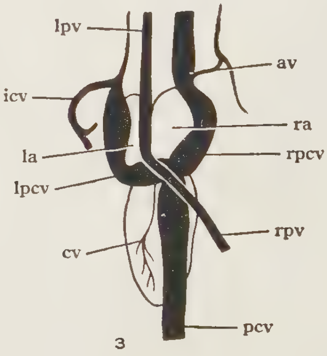


Fig. 1.—Heart of *T. ligatus*, ventral aspect: *av*, azygos vein; *la*, left auricle; *lca*, left carotid artery; *lpa*, left pulmonary artery; *lpcv*, left precaval vein; *lpv*, left pulmonary vein; *lsa*, left systemic arch; *pa*, pulmonary arch; *ra*, right auricle; *rca*, right carotid artery; *rpcv*, right precaval vein; *rsa*, right systemic arch; *tg*, thyroid gland; *v*, ventricle.

Fig. 2.—Heart of *T. polygrammicus*, left lateral aspect: *ava*, anterior vertebral artery; *da*, dorsal aorta; *ica*, intercostal arteries; *pcv*, postcaval vein; *pl*, posterior lung; *rpv*, right pulmonary vein.

Fig. 3.—Heart of *T. ligatus*, dorsal aspect: *cv*, coronary vein.

Fig. 4.—Heart of *T. polygrammicus*, ventral wall removed: *apv*, aperture of pulmonary vein; *ava*, auriculo-ventricular aperture; *cva*, cavum arteriosum; *cvv*, cavum venosum; *ias*, inter-auricular septum; *ivs*, interventricular septum; *saa*, sinu-auricular aperture.

The blood passes from the sinus venosus to the right auricle by way of the elongate, obliquely placed sinu-auricular aperture, which is situated posteriorly and dorsolaterally in the roof of the right auricle (Fig. 4). The aperture is guarded along each edge by a valve which projects into the auricle. The valve on the posterior border of the aperture is continued obliquely forwards to form a muscular ridge which extends to the apex of the auricle. The two valves cross over each other in closing, the posterior valve being dorsal to the anterior valve at the mesial end and ventral to it at the lateral end.

(ii) *The Auricles.*—The right auricle is larger than the left, and darker in colour. It is very clearly separated externally from the ventricle by the transverse coronary sulcus, and, at its lower right margin, extends as a pouch down over the anterior end of the ventricle. The two auricles are widely separated from each other at their anterior ends. The cavity of the right auricle is wide and long. Its dorsal wall is thin, but the ventral, mesial, and lateral walls are somewhat honeycombed with muscular trabeculae. The sinu-auricular aperture in the dorsal wall, and the ridge-like extension of its posterior valve have already been described. The right auricle receives the blood from the sinus venosus and delivers it to the ventricle.

The left auricle is smaller and does not overlap the ventricle. The left auricle receives the pulmonary blood; just before reaching the heart the two pulmonary veins become confluent, and enter the dorsal surface of the left auricle very obliquely by this common vessel. The pulmonary aperture is circular and situated towards the posterior mesial border of the auricle, and is not equipped with any valvular device (Fig. 4).

The interauricular septum is thin, complete, and vertically placed and when relaxed projects into the left auricle. It has a crescentic posterior border, along the margin of which are attached two large flap-like valves, one on either side, which guard the two auriculo-ventricular apertures. The free edges of the valves are not attached to the wall of the ventricle by chordae tendineae, but depend freely into the ventricular cavity. Hence, as Kashyap points out, the two valves are pushed towards the median line during the auricular systole when the blood is passing from the auricles to the ventricle and, when the ventricle contracts, the valves fill with blood and are pushed up so that their free margins are laterally extended, and prevent the flow of blood back into the auricles.

(iii) *The Ventricle.*—This is rather elongated and has a bluntly rounded posterior tip. It is divided longitudinally into a smaller, darker, right portion receiving the venous blood from the right auricle, and a slightly larger, paler, left portion receiving arterial blood from the pulmonary vein via the left auricle. The line which separates these two regions of the ventricle passes obliquely backwards on the ventral surface of the left of the roots of the arterial arches to a point just to the right of the apex of the ventricle. As is indicated by the colour of the walls of the ventricle, the left wall is somewhat thicker than the right.

Internally, the ventricular cavity is incompletely divided into two portions—the cavum arteriosum on the left, and the cavum venosum on the right—by a septum, which like the ventricular walls, is made up of a dense network of muscular trabeculae (Fig. 4). This septum begins in the posterior region of the ventricle, on the right side, and passes forwards dorsoventrally, its course being marked externally by the line which divides the ventricle into left and right regions. The septum, which is much thicker caudally than it is cranially, does not extend right to the anterior region of the ventricle, hence the two chambers are confluent immediately behind the auricles. The two cavities of the ventricle are of almost equal dimensions. A ventral cavum pulmonale is present as a small pouch, which is in free communication with the cavum venosum proper, there being no dividing ridge or septum, such as Rau (1924) and Mathur (1946) describe in *Eunectes murinus* and *Natrix piscator* respectively. The cavum pulmonale has few muscular trabeculae in its wall, a feature which helps to distinguish it from the cavum venosum.

(*b*) *The Aortic Arches*

Goodrich (1919) describes the interventricular septum of the reptilian heart as dividing the ventricle "into a left cavity leading to the base of the right systemic arch, and a right cavity leading to the base not only of the pulmonary, but also of the left systemic arch." In *Typhlops*, however, the three aortic arches arise from the cavum venosum. The pulmonary arch originates from a point at which the interventricular septum is complete, but the two systemic arches arise somewhat more anteriorly where the left and right ventricular cavities are confluent. The right systemic arch arises slightly in front of the left; each arch is guarded at its base by two pocket valves.

(i) *The Pulmonary Arch* (Figs. 1 and 13).—This arises from the ventricle in the centre of the anterior border on the ventral surface. It passes forwards on the left of the systemic arches as far as the anterior border of the auricles, then curves to the right, and divides in two above the systemic arches. One branch passes back above the heart, curves around on the dorsal surface of the posterior lung, and extends to the very tip of this organ, giving off an extensive network of vessels to the lung tissue (Fig. 14).

The second branch of the pulmonary arch forms the pulmonary artery to the anterior (left) lung. The vessel passes forwards along the right ventrolateral aspect of this structure, embedded in a groove in the lung tissue. This is a much more substantial vessel than its counterpart to the lower lung, and it gives off a very large number of branches both to the surface and interior of the anterior lung (Fig. 13).

(ii) *The Systemic Arches* (Figs. 1 and 2).—The right systemic arch arises from the ventricle on the right of, and dorsal to, the pulmonary arch, its base being largely obscured by the left systemic arch. The right arch passes forwards and obliquely to the right; somewhat anterior to the auricles it curves around the base of the anterior lung, and turns backwards and upwards to a position above the auricles, where it unites with the left systemic arch to form the median dorsal aorta (Fig. 2).

Before uniting with the left systemic arch, the right vessel gives off the following branches:

(i) Coronary arteries.
(ii) Primary carotid, or right and left common carotid arteries.
(iii) Anterior vertebral artery.
(iv) Four intercostal arteries.

These vessels are described later.

The left systemic arch arises from the ventricle to the right of, and ventral to, the right systemic arch, and crosses the latter ventrally at the anterior border of the auricles (Fig. 1). It then curves around, upwards and backwards, and in the mid-dorsal line unites with the right systemic arch. No trace of a ductus arteriosus was found on either side of *Typhlops*. This is an interesting point, since, according to O'Donoghue (1917), ophidians normally have a ligament on each side, representing the ductus arteriosus. The complete absence of such structures is characteristic of the Sauria.

(*c*) *Arteries arising from the Right Systemic Arch*

(i) *The Coronary Arteries.*—These arise from the right systemic arch shortly after its origin. One supplies the ventral, and the other the dorsal surface of the heart.

(ii) *The Origin of the Left and Right Common Carotid Arteries.*—This varies somewhat between individuals. In some, a very short, primary carotid artery arises from the right systemic arch just anterior to the auricles, and this primary carotid then immediately divides into right and left common carotid arteries. In other individuals the right, then the left, common carotid arteries arise directly from the systemic. In *T. polygrammicus* and *T. australis* one common carotid artery is frequently appreciably stouter than the other (Fig. 2). In *T. proximus* and *T. ligatus* the two common carotid arteries are more often equal in size (Fig. 1). However they arise, the distribution of the two common carotid arteries is as follows:

(1) The left common carotid artery passes obliquely across the base of the anterior lung and then turns forwards along the left ventrolateral aspect of that organ. It gives off small arteries to the thymus and thyroid glands as it passes.

(2) In the anterior region of the body, just behind the head, the left common carotid artery divides into the internal and external carotid arteries; the former disappears into the head region, and the latter breaks up into a number of fine branches which supply the tongue muscle, the trachea, gut, and jaw muscles.

(3) The right common carotid artery passes forwards bound closely to the right precaval vein, and gives a small branch to the right portion of the thymus gland in passing. In the region just behind the head it divides in much the same way as does the left common carotid artery.

Ray (1934), in discussing the primary carotid of *Ptyas mucosus*, says "[It] is not absent here as in some snakes, for instance Boa, in which this trunk is totally

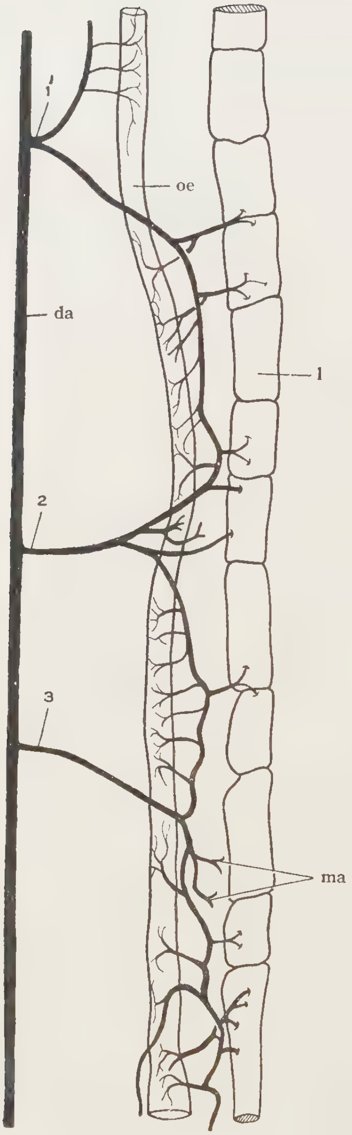


Fig. 5

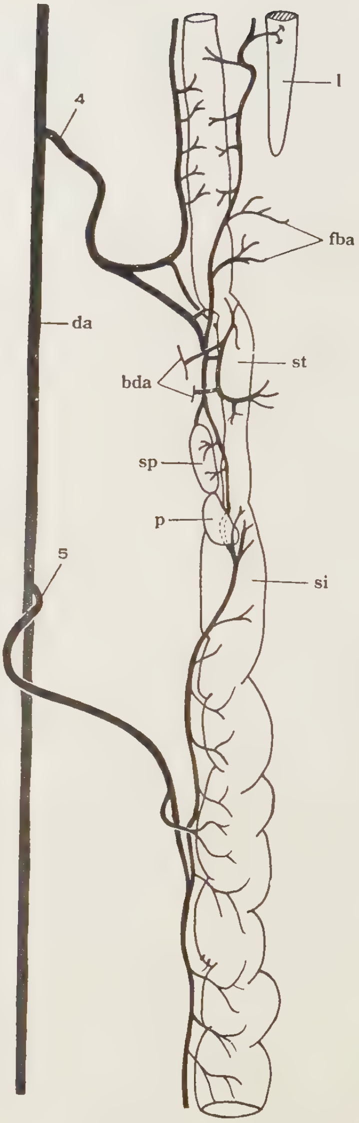


Fig. 6

Fig. 5.—Distribution of the first, second, and third hepato-oesophageal arteries in *T. polygrammicus*: *da*, dorsal aorta; *l*, liver; *ma*, arteries to mesentry; *oe*, oesphagus; *1, 2, 3*, first, second, and third hepato-oesophageal arteries.

Fig. 6.—Distribution of the lieno-gastric and superior mesenteric arteries in *T. polygrammicus*: *bda*, arteries to bile duct; *da*, dorsal aorta; *fba*, arteries to fat-body; *l*, liver; *p*, pancreas; *si*, small intestine; *sp*, spleen; *st*, stomach. *4*, lieno-gastric artery; *5*, superior mesentric artery.

absent, and as such the common carotids arise separately from the right systemic." But as both conditions are found within the genus *Typhlops*, it is possible that the same variation may occur within other genera of reptiles, and may not present a group characteristic such as Ray would seem to suggest.

Bellairs and Underwood (1951), in commenting on the frequent suppression in snakes of the greater part of the right carotid artery, say that in such cases this vessel is represented only by the artery to the thyroid gland, and that the blood supply to the head is derived from a single primary carotid artery which arises from the right systemic arch, and passes up the neck as the left carotid. It communicates by a transverse anastomosis with the persistent cranial portions of the right carotid artery just behind the head. The condition of the carotid arteries in *Typhlops* does not fit into the pattern of the above generalized description, and the thyroid gland is supplied by the left common carotid.

(iii) *The Anterior Vertebral Artery.*—This artery arises from the right systemic arch at the point where the latter turns backwards in the mid-dorsal region above the heart, and a short distance before it unites with the left systemic arch (Fig. 2).

The anterior vertebral artery passes forwards in the mid-dorsal line, gradually diminishing in diameter, to a point just behind the head, where it passes ventrally over the left common jugular vein, then disappears into the body wall, still in the mid-dorsal line. All along its length it gives off, at regular intervals, short intercostal arteries which divide in two and enter the body wall slightly to the left and right of the mid-line. These intercostal arteries arise singly, and number approximately 45.

(iv) *Four Intercostal Arteries.*—These arise behind the origin of the anterior vertebral artery, and in front of the junction of the two systemic arches (Fig. 2). They are rather longer than the intercostal arteries given off by the anterior vertebral artery, but, like them, arise singly and divide into two branches which enter the body wall to the left and right of the vertebral column.

(*d*) *Vessels arising from the Dorsal Aorta*

Throughout its length from the region above the heart, to its termination above the cloaca, the dorsal aorta gives off a very large number of intercostal arteries. These are similar to those described above, but in the central third of the body are somewhat larger than the intercostals of the anterior region.

Figures 5, 6, and 7 show the distribution of the arteries arising from the dorsal aorta which supply the viscera. As can be seen, longitudinal systems are very much in evidence in *Typhlops*, where, as in many reptiles, the alimentary canal, the liver, gonads, and fat-body all have longitudinal vessels which are supplied by a series of branches from the dorsal aorta. Especially in the more posterior region of the body, extensive networks of vessels may be formed, sometimes linking up two or more of the longitudinal systems. The arteria epiploica, for example, receives branches from the dorsal aorta and from the spermatic, renal, and oviducal arteries.

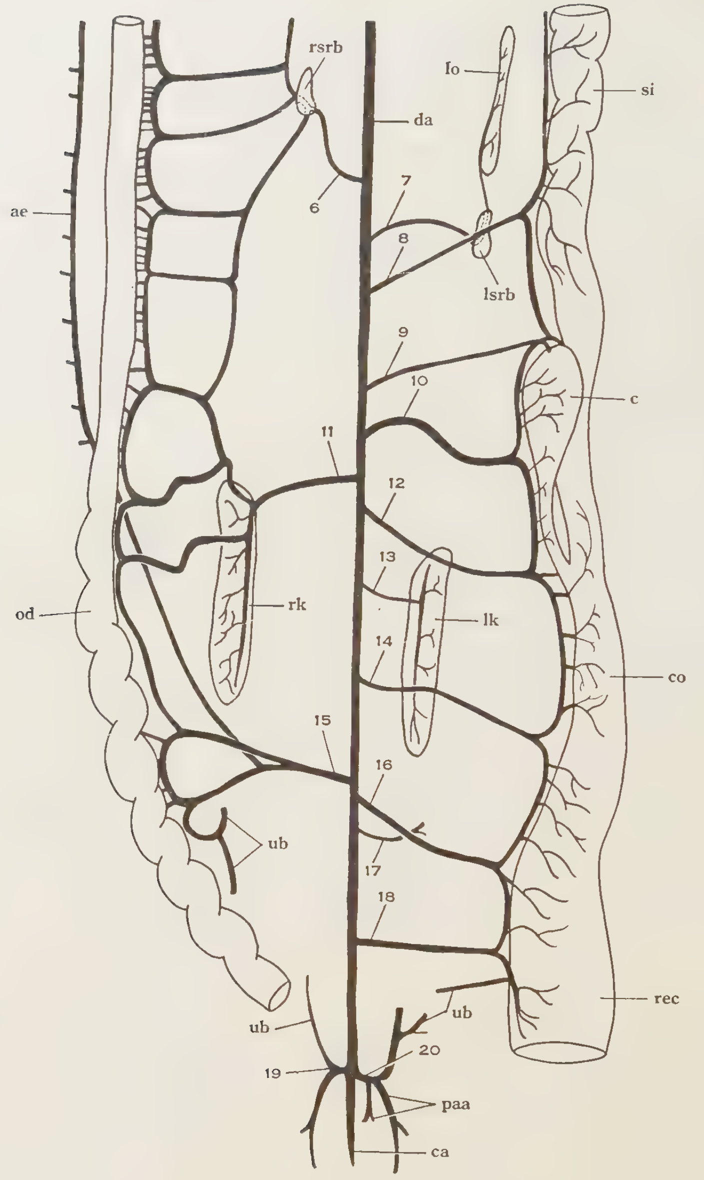


Fig. 7.—Distribution of arteries arising from the posterior region of the dorsal aorta in *T. polygrammicus*: *ae*, arteria epiploica; *c*, caecum; *ca*, caudal artery; *co*, colon; *da*, dorsal aorta; *lk*, left kidney; *lo*, left ovary; *lsrb*, left suprarenal body; *od*, oviduct; *paa*, arteries to postanal region; *rk*, right kidney; *rsrb*, right suprarenal body; *si*, small intestine; *ub*, ureterine branches. *6*, right ovarian artery; *7*, left ovarian artery; *8*, first inferior mesenteric artery; *9*, second inferior mesenteric artery; *10*, third inferior mesenteric artery; *11*, right renal artery; *12*, fourth inferior mesenteric artery; *13*, left renal artery; *14*, first rectal artery; *15*, posterior oviducal artery; *16*, second rectal artery; *17*, left ureterine artery; *18*, third rectal artery; *19*, right postanal artery; *20*, left postanal artery.

(*e*) *The Venous System*

(i) *The Anterior Vessels*

The venous system in the anterior region of the body is very complex and certainly does not conform to the usual pattern of the vessels in this region of other reptiles: in fact, its abnormal arrangement poses one or two problems of nomenclature.

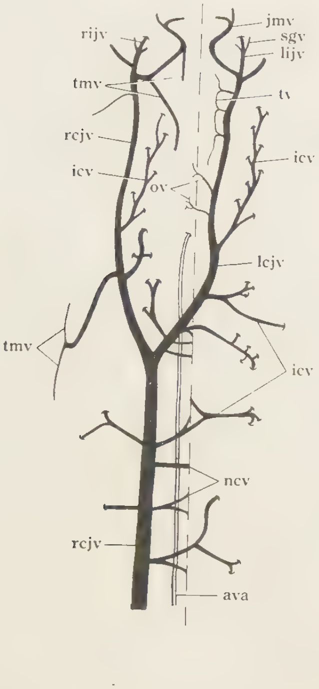


Fig. 8

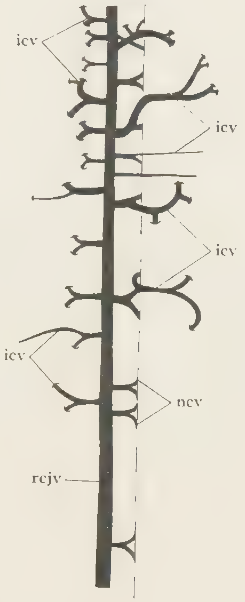


Fig. 9

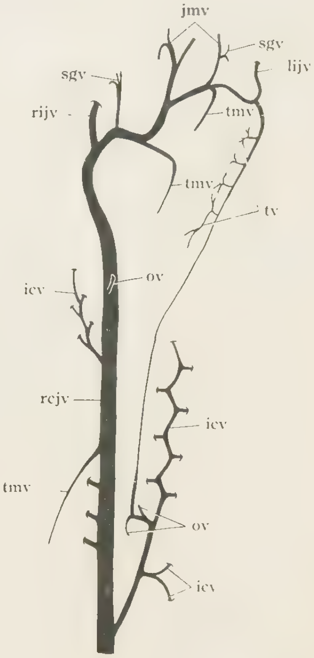


Fig. 10

Fig. 8.—*T. polygrammicus*, anterior venous system: *ava*, anterior vertebral artery; *icv*, intercostal veins; *jmv*, veins from jaw muscles; *lcjv*, left common jugular vein; *lijv*, left internal jugular vein; *ncv*, veins from neural canal; *ov*, veins from oesophagus; *rcjv*, right common jugular vein; *rijv*, right internal jugular vein; *sgv*, veins from salivary glands; *tmv*, veins from tongue muscles; *tv*, veins from trachea. Broken line represents mid-dorsal line of body cavity.

Fig. 9.—*T. polygrammicus*, tributaries of the right common jugular vein in region anterior to the heart: *icv*, intercostal veins; *ncv*, veins from neural canal; *rcjv*, right common jugular vein. Broken line represents mid-dorsal line of body cavity.

Fig. 10.—*T. australis*, anterior venous system. *icv*, intercostal veins; *jmv*, veins from jaw muscles; *lijv*, left internal jugular vein; *ov*, veins from oesophagus; *rcjv*, right common jugular vein; *rijv*, right internal jugular vein; *sgv*, veins from salivary glands; *tmv*, veins from tongue muscles; *tv*, veins from trachea.

In *T. polygrammicus* (Figs. 8 and 9) the right and left common jugular veins are formed in the usual manner by the union of the several vessels which, on each side of the body, drain the jaw muscles, the salivary glands, the tongue muscle, and the brain. The right common jugular vein continues straight back towards the heart as a very stout vessel lying in the dorsolateral aspect of the body cavity, above the right carotid artery, and close to the anterior lung. It receives further vessels from the retractor muscle of the tongue, from the body wall, and from the gut.

The left common jugular vein follows a similar course for a very short distance, receiving a large tributary, formed by the union of several intercostal vessels; and two or three oesophageal vessels. After following briefly along the left dorsolateral aspect of the alimentary canal, the left common jugular vein curves upwards to the dorsal wall of the body cavity. It receives a well-defined tracheal vein, and three or four intercostal veins. It then curves around to the right, passes dorsal to the anterior vertebral artery, and receives three smaller intercostal veins. Finally, it unites with the right common jugular vein.

The right common jugular vein then continues back towards the heart, receiving as it does so a series of intercostal veins draining the body wall and neural canal. These intercostal veins are from both sides of the body, and their mutual arrangement, and the pattern of their junction with the right common jugular vein, is quite irregular. The intercostal veins from the right side of the body are more numerous than are those from the left, but the latter are considerably stouter than the former. The majority of the intercostal veins are formed by the junction of one or more vessels from the parieties with one from the nerve cord, and sometimes one from the gut. The right common jugular vein receives a small vessel from the right portion of the thymus gland as it passes that organ.

Just before the right common jugular vein enters the sinus venosus as the right precaval vein, it receives the azygos vein. This latter vessel is very short and is formed by the union of the anterior and posterior azygos veins at a point level with the right auricle (Figs. 1 and 3).

Posterior to the point where the left common jugular vein passes across to the right of the body cavity, a very fine vein arises on the left and passes back towards the heart intimately bound to the left carotid artery. It receives a few very small tributaries from the oesophagus, and one from both the thyroid and thymus glands. Just anterior to the heart it receives a large intercostal vein, and becomes a stout, well-developed vessel (Figs. 1 and 3); from here to its entry into the sinus venosus it is regarded as the left precaval vein. Immediately prior to its entry into the sinus venosus it receives the coronary veins.

The absence of subclavian veins introduces some uncertainty as to the correct terminology for the posterior regions of the anterior veins; O'Donoghue (1912) dispenses with the term "precaval" entirely, and speaks of the sinus venosus being formed of the left and right common jugular veins and the postcaval vein. In view of the complex disposition of the various anterior veins of *Typhlops*, however, the use of the term "precaval" is considered to be warranted.

In *T. australis* (Fig. 10) the arrangement of the anterior veins is quite different. In this species, all the veins from the head, jaw, and tongue muscles, salivary glands, and the anterior region of the oesophagus join to form a stout vessel which passes obliquely and ventrally from left to right in the anterior region of the body cavity, and which on reaching the right side of the body cavity turns abruptly backwards as the relatively enormous right common jugular vein.

The only trace of the left common jugular vein is a small vessel which arises in the body wall, and passes back for a short distance, receiving a series of intercostal veins, and one or two small veins from the trachea and oesophagus. It then crosses dorsally to the right side of the body cavity, above the anterior vertebral artery, and unites with the right common jugular vein. The last tributary it receives from the gut and trachea has a very long, fine connection with one of the short veins draining the muscles of the head.

Posterior to the junction of the vessel from the left side of the body with the right common jugular vein, the latter continues back to the heart, receiving similar tributaries to its counterpart in *T. polygrammicus*.

(ii) *The Posterior Vessels*

(1) *The Postcaval System* (Fig. 11).—Many small veins arising in the tissue of the right kidney unite on the inner side of its convex border to form the right efferent renal vein, which passes forwards in the body cavity, and receives numerous short fine vessels from the right suprarenal body as it passes that organ.

A similar vein, the left efferent renal vein, arises from the left kidney, and passes along the left suprarenal body, receiving many tributaries from it. It continues past the left testis, receiving several spermatic veins as it does so, then bends towards the right, and unites with the right efferent renal vein.

This results in the formation of the postcaval vein, which continues forwards past the right testis, receiving spermatic veins therefrom. On reaching the posterior tip of the liver it becomes embedded in a groove along the ventral surface of that organ, and receives a few small hepatic veins from the superficial regions.

The course of the postcaval vein along the surface of the liver is a rather tortuous one, and for part of its course the vein becomes almost completely enclosed in the liver tissue.

A short distance from the anterior end of the liver the postcaval vein emerges more onto the surface of the organ and receives three or four stout hepatic veins. It then passes to the dorsal surface of the heart and enters the sinus venosus.

In the female, the formation of the postcaval vein differs slightly from the above description. The origin of the left and right efferent renal veins is as described above. On leaving the kidney, however, the vein on the right receives several vessels from the oviduct before passing the suprarenal body and collecting the tributaries therefrom.

The left efferent renal vein passes and drains the left suprarenal body, then reaches the base of the left ovary, and lies along its inner border for the posterior third of its length, receiving several small vessels from the ovary. The vein then curves to the right and unites with the right efferent renal vein, thus forming the postcaval vein. This receives the vessels from the anterior two-thirds of the right ovary, and from the entire length of the left ovary.

The course of the postcaval vein from here to the sinus venosus is the same as described for the male.

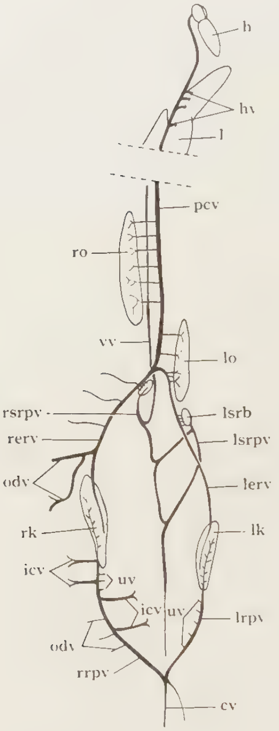


Fig. 11

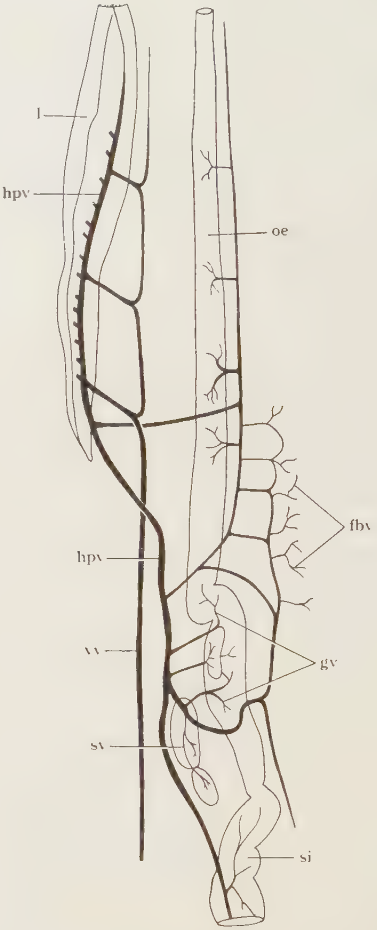


Fig. 12

Fig. 11.—Postcaval system, renal portal system, and suprarenal portal system of female: *cv*, caudal vein; *h*, heart; *hv*, hepatic veins; *icv*, intercostal veins; *l*, liver; *lerv*, left efferent renal vein; *lk*, left kidney; *lo*, left ovary; *lrpv*, left renal portal vein; *lsrb*, left suprarenal body; *lsrpv*, left suprarenal portal vein; *odv*, oviducal veins; *pcv*, postcaval vein; *rerv*, right efferent renal vein; *rk*, right kidney; *ro*, right ovary; *rrpv*, right renal portal vein; *rsrpv*, right suprarenal portal vein; *uv*, ureterine veins; *vv*, vertebral vein.

Fig. 12.—Hepatic portal system: *fbv*, veins from fat-body; *gv*, gastric veins; *hpv*, hepatic portal vein; *l*, liver; *oe*, oesophagus; *si*, small intestine; *sv*, splenic vein; *vv*, vertebral vein.

(2) *The Renal Portal System* (Fig. 11).—The caudal vein arises in the posterior extremity of the body by the confluence of several tiny vessels from the body wall, and from the vertebral column. In the region immediately behind and above the cloaca the caudal vein receives tributaries from the scent glands, hemipenes, etc. and then divides into two small vessels, the left and right renal portal veins.

The vein on the left passes forwards associated with the ureter, from which it receives many fine vessels, and on reaching the kidney, passes on to its inner surface near the ventral border, gradually breaking up in the kidney tissue.

The right renal portal vein receives vessels from the body wall and several from the ureter; in the female, from the oviduct also. It then disperses into the tissue of the kidney.

(3) *The Suprarenal Portal System* (Fig. 11).—In the posterior region of the body blood from the intercostal and neural veins flows into the vertebral vein. This latter is a longitudinal vessel lying very close to the body wall, immediately to the left of the vertebral column when it first arises, but later crossing over to the right.

On reaching the level of the anterior border of the left kidney, the vertebral vein gives rise to the left suprarenal portal vein, by two branches, which actually interrupt the course of the vertebral vein. The left suprarenal portal vein passes obliquely downwards and forwards in the body cavity, and just before it reaches the suprarenal body it receives a further branch from the vertebral vein.

The right suprarenal portal vein arises in the same way from the vertebral vein. It does not receive a second branch.

The left and right suprarenal portal veins each break up in the tissue of the suprarenal body of the same side, and the blood from them is passed into the corresponding efferent renal vein.

The vertebral vein continues forwards just to the right of the vertebral column, very closely applied to the body wall.

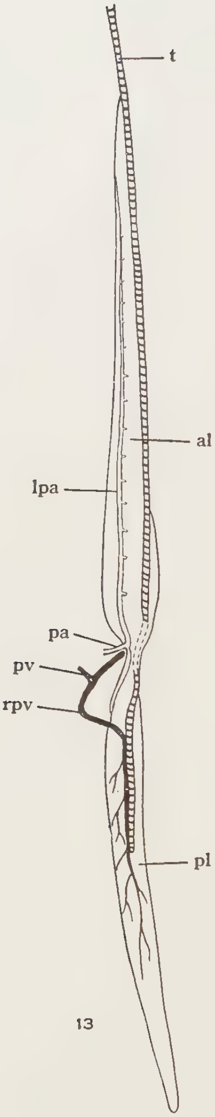
In *T. australis*, the vertebral vein appears to be broken up into three stout, longitudinal vessels, two of which are associated with the suprarenal bodies, and one with the liver.

(4) *The Hepatic Portal System* (Fig. 12).—The hepatic portal vein begins as a very fine vessel on the dorsal wall of the rectum, and gradually increases in size as it passes forwards and receives tributaries from the wall of the intestine. Although the gut may be convoluted in this region, the vein maintains a straight course.

The fat-body is drained by an anterior and a posterior vein, which lie in the mesentery along the length of the fat-body, and join at the level of the pancreas. The vein thus formed turns upwards to join the hepatic portal vein, and it unites with small vessels draining the pancreas and gut wall as it passes.

The hepatic portal vein continues forwards, collecting more small veins from the gut wall, and also a long vein draining the oesophagus.

On reaching the posterior tip of the liver, the hepatic portal vein passes on to the dorsal surface of that organ, and receives firstly a short, stout vein, which is a cross-connection from the oesophageal vein; and secondly the first of three stout vessels, which come from the vertebral vein, in the mid-dorsal line. Immediately after receiving this vessel, the hepatic portal vein begins to break up in the tissue of the liver, though it is still visible as a very thin vessel, almost to the anterior tip of the liver.



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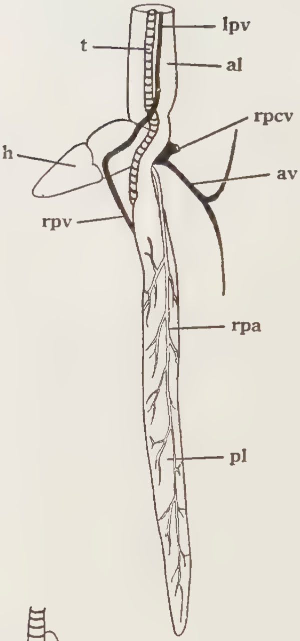

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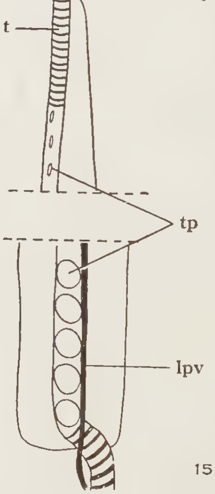

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Fig. 13.—Respiratory system: *al*, anterior lung; *lpa*, left pulmonary artery; *pa*, pulmonary arch; *pl*, posterior lung; *pv*, pulmonary vein; *rpv*, right pulmonary vein; *t*, trachea.

Fig. 14.—Posterior lung and heart, dorsal aspect: *av*, azygos vein; *h*, heart; *lpv*, left pulmonary vein; *rpa*, right pulmonary artery; *rpcv*, right postcaval vein.

Fig. 15.—Anterior and posterior sections of anterior lung, with part of ventral wall of trachea removed, showing tracheal perforations (*tp*).

The second of the vessels from the vertebral vein enters the hepatic portal vein about one-quarter of the length of the liver from the posterior end, and the third one about one-half of the way along.

(iii) *The Pulmonary Veins* (Figs. 2, 3, 13, and 14)

The two pulmonary veins unite before entering the right auricle.

The pulmonary vein from the anterior lung is very distinct; it arises at the anterior end of the lung, on the left side, and immediately dorsal to the trachea. It rapidly increases in diameter as it passes back, and receives numerous tributaries from the lung. It becomes set in a groove along the left ventrolateral aspect of the lung, and remains so placed until it reaches the posterior end of this organ. It then curves slightly to the right, and passes to the dorsal surface of the heart. Here, at the posterior border of the right auricle, it unites with the pulmonary vein from the posterior lung (Figs. 3 and 14).

The pulmonary vein from the posterior lung arises approximately half way along that organ, just beyond the termination of the trachea (Fig. 13). The vein is formed by the junction of several very fine vessels, and for a short distance continues forward along the ventral surface of the lung, receiving many tributaries as it does so. It leaves the lung at a point above the ventricle and passes ventrally to join its fellow on the dorsal surface of the right auricle.

IV. The Respiratory System

The respiratory system of *Typhlops* is distinctly anomalous, and not at all in accord with the description given by Waite (1918). He remarks, "The blind snakes have only one true lung; it is placed on the right side and extends from the heart to the liver. Another organ, the so-called tracheal lung, regarded by some as the vestige of a once functional lung, is without cavity, is composed of cells of different sizes, and appears to have no communication with the trachea or the lung. It has been suggested that this structure may not be a pulmonary organ."

As will be seen from the following description, the animals dissected did not conform to the above in a single feature.

The elongated respiratory sac is extended throughout the anterior half of the body cavity, and is conspicuously divided into two subequal parts by a narrow constriction (Fig. 13), which is, however, canalized. A clue to the interpretation of this condition would seem to be afforded by the blood vessels.

The pulmonary arch, shortly after its origin, divides into two pulmonary arteries, one going to each portion of the lung sac (Fig. 13). The artery supplying the anterior portion passes forwards along the right ventrolateral aspect of the lung embedded in a deep groove. It reaches to the anterior extremity of the lung, and throughout its length gives off numerous branches which ramify over the surface of the lung, and through the lung tissue. This anterior (left) pulmonary artery is by far the more substantial vessel of the two. The right pulmonary artery passes back and curves around to the dorsal surface of the posterior portion of the lung, to which it supplies an extensive network of vessels.

After circulating through the respiratory tissue, the blood is returned to the heart by the left and right pulmonary veins. The former arises at the anterior end of the lung and passes back down the left lateral aspect of that organ, rapidly increasing in diameter as it receives further tributaries. On reaching the posterior end of this portion of the lung, the vein curves to the right and, on the dorsal surface of the heart, unites with the right pulmonary vein. This latter vessel arises approximately half-way along the posterior portion of the lung, on its ventral surface. It is formed by the confluence of several small veins, and for a short distance it passes forward along the surface of the lung, receiving many tributaries. It does not extend right to the anterior end of this portion of the lung, but on reaching a point above the ventricle, it passes ventrally in the body cavity to unite with its fellow, and thus forms the common pulmonary vein, which enters the left auricle (Figs. 3 and 14).

From these vascular arrangements it would seem, therefore, that there is, in effect, a displacement of the right lung behind the left. This, after all, would be an extreme example of the trend towards elongation and asymmetry which commonly pertains to the organs of many reptiles.

The anterior lung (Figs. 13 and 15) begins narrowly close behind the buccal cavity, and increases gradually in diameter throughout its length; it ends immediately in front of the heart. Externally it is smooth and rounded; it is a well-developed structure, spongy, elastic, and yet relatively firm to the touch. It occupies the greater part of the body cavity anterior to the heart. At its posterior extremity it is bluntly rounded on the right, and on the left is continued back above the heart as a short, narrow tube of respiratory tissue, which soon expands into the posterior lung.

The posterior lung (Fig. 14) is not quite as long as the anterior organ; it lies on the right side of the body cavity, dorsal to the liver. It is soft and hollow, with very thin, almost transparent walls. It reaches its maximum diameter in the first third of its length, and tapers very gradually to end in a bluntly rounded point.

The larynx is a dome-shaped prominence on the floor of the buccal cavity immediately behind the tongue pouch. This prominence is formed by two cartilages, each shaped as a hollow quarter-sphere, which are in close contact along their mesial borders in the posterior half of the dome, but which do not meet in the anterior half. Thus the glottis is a median longitudinal slit, extending from the apex of the dome to the floor of the buccal cavity.

The trachea extends from the posterior limit of the larynx to a point slightly less than half way along the posterior lung. The trachea lies along the left side of the anterior lung, embedded in a groove in the lung tissue. It passes to the ventral surface of the posterior lung, by way of the narrow constriction mentioned above, and gradually decreases in diameter before finally disappearing about half way along this organ. From the buccal cavity to the anterior tip of the lung, the tracheal wall is complete, and is supported by complete rings of costal cartilage.

Once the trachea reaches the lung, however, and becomes partially embedded in the lung tissue, only the exposed portion of the wall has cartilagenous supports, which are, of course, semicircular. Also, that part of the tracheal wall in contact with the lung becomes highly perforated (Fig. 15): at first the lumen of the trachea is placed in communication with the cavity of the lung by a series of small, rather slit-like apertures in the tracheal wall, each aperture being separated from its neighbours by an appreciable area of tracheal wall.

As the trachea extends further along the lung the perforations become gradually larger and more circular, and separated from one another only by a narrow strip of wall supporting a branch of the pulmonary artery. By the time the trachea reaches the base of the anterior region of the lung, the perforations have reached quite enormous proportions—they are oblong rather than circular, and are separated by extremely thin strips of tissue.

In the posterior lung, there is little sign of such perforation—rather, the wall of the trachea adjacent to the lung has disappeared, and apart from three or four branches of the pulmonary artery which extend across it, the tracheal lumen is in continuous communication with the lung cavity.

The anterior lung is, as previously mentioned, very spongy and elastic. It is very narrow at its forward end, and widens steadily towards its base. Internally, the lung has a rather remarkable honeycomb-like appearance macroscopically; its substance is composed largely of a complicated network of blood vessels from the pulmonary artery and vein, ramifying through delicate connective tissue. The general effect is of a series of large, rounded cavities or bronchioles extending transversely across the lung from the tracheal perforations, and each opening laterally into a further series of smaller and smaller alveoli. This subdivision of the lung becomes gradually less complicated towards the base of the anterior portion, and is only moderately developed in the connection between anterior and posterior regions. It soon disappears entirely in the posterior lung.

The posterior lung at first widens rather sharply, then tapers off gradually to a point. For the greater part it is merely a membranous sac with a gradually diminishing network of blood vessels in its walls. There is a very poorly developed area of "honeycombing" at the anterior end, formed mainly by the inward protrusion of the blood vessels.

Although the two parts of the lung of *Typhlops* differ so much in their general structure, there seems little doubt that both have a respiratory function and that the so-called "tracheal" lung, far from being functionless and vestigial, is in fact the main respiratory organ. This suggestion is supported by the presence of the large and numerous apertures leading from the trachea into this lung, and by the very extensive network of capillaries from both pulmonary artery and vein which forms such a major part of the lung tissue.

The posterior lung may act to some extent as an air reservoir, especially when the animal is burrowing in sandy ground, where soil air would be relatively scarce. Varde (1951) points out that the very elongated and saccular lung of some aquatic snakes functions in this manner, thus enabling the animals to remain submerged for considerable periods of time.

Varde states that morphologically, there are three distinct trends in pulmonary evolution of the snakes. The most simple trend shows the retention of the paired condition of the lungs with full dimensions. This condition is seen in the pythons, where both right and left lungs are present, lying side by side in the body cavity. Neither is remarkably saccular. There is a common pulmonary vein, which passes between the two lungs and receives tributaries from either side. The second trend shows the suppression of the left lung and the extraordinary development of the right one, which may extend as far as the cloaca in extreme cases. The third trend shows an anterior extension of the lung, with the trachea incorporated into it; such a condition is seen in many vipers. Varde, unfortunately, does not give any details of the pulmonary circulation in such types, nor does she describe the anterior tracheal lung, so it is not possible to compare the respiratory system of vipers with that of *Typhlops*.

In most snakes, where the modification of the respiratory system has taken the form of the partial or complete suppression of one lung, only one pulmonary artery and vein develop. But in *Typhlops* both the left and right pulmonary arteries and veins are well developed, thus providing another piece of evidence to support the conclusion that both lungs are functional. Finally, in all the specimens dissected, air was definitely present in both lungs.

In the absence of developmental studies, it is not possible to do more than speculate on the means whereby this condition of the lungs has come about. However, the following hypothesis is tentatively suggested as a possible (but unproven) sequence of events.

It is suggested that in response to the need for elongation of organs in the body cavity, the lungs ceased to lie side by side, and gradually came to lie one behind the other. In this condition the bronchus of the posterior lung (in this case the right lung) would be greatly elongated, and would need to pass along the entire length of the left lung in order to reach its destination. Thus in time the right bronchus could become embedded in the tissue of the left lung, and by the development of a series of perforations in its dorsal wall, could supply air to that organ. Once this condition had become established, the left bronchus would be redundant and might well atrophy, leaving the right bronchus to conduct air to both lungs.

It is perhaps significant that the sacculation of the anterior lung of *Typhlops* extends along the whole length of the organ, and appears to be greatest along the line of the trachea; while in the posterior lung, which the trachea enters in a more normal fashion, the sacculation is restricted to that part of the wall immediately adjacent to the point of entry of the trachea.

Modification of the respiratory organs along these lines would be in accordance with a law that is often seen in operation in the animal world—the law of the economy of tissue, whereby useless parts are eliminated, or modified for purposes other than those for which they were originally developed.

V. The Renal–Reproductive System

(*a*) *Female* (Figs. 16–20)

(i) *The Right Ovary, Kidney, and Suprarenal Body*

These are further forward in the body cavity than are the corresponding organs of the left (Fig. 16). The right kidney is slightly larger than the left, but the two ovaries appear to be of approximately equal size, though the right ovary may be very slightly the larger of the two. There is, however, only one functional oviduct, and that is the right one. The left oviduct has completely atrophied.

While the partial or complete atrophy of some or all of the reproductive organs on one side of the body of the female is fairly widespread in some vertebrate groups (e.g. in the selachians, Myliobatidae, and birds), it does not occur to any great extent among the reptiles. M. J. Burt (quoted by Guibe (1948)) counted the number of embryos in each oviduct of various species of Colubridae, and found that with *Thamnophis sirtalis* and *T. sauritus* the right oviduct always contained more embryos than the left. He concluded that "this suggests that the left oviduct may be in the process of evolutionary decline." In view of the condition in *Typhlops*, it would be of interest to have more detailed information concerning the relative development of the right and left reproductive organs of other reptiles.

The kidneys are rather elongate, bean-shaped structures, light brown in colour, and with the inner surface flattened and slightly concave, and the outer surface convex. They are orientated in the body cavity with their concave border ventrally directed, and the convex border close to the dorsal aorta. The kidneys are markedly lobulated, with deep irregular fissures marking both surfaces, and dividing each kidney into approximately eight sections.

The ureters are very wide tubes with thin membranous walls. They arise on the mesial surface of the kidneys, near the anterior end, and as they pass backwards are supplied by numerous fine tubules from the kidney tissue. Each ureter becomes slightly distended just before entering the cloaca. The two ureters do not at any time form a common duct, though they do become fused by their mesial walls, in the region immediately anterior to the cloaca (Fig. 18). The two ureters open into the cloaca by separate papillae on its dorsal wall, just behind the oviducal aperture. These urinary paillae are short, stout projections which bend outwards away from each other, and each opens by a small V-shaped slit on the tip (Figs. 16 and 20).

The ovaries (Fig. 16) are long and narrow and are suspended by the mesovarium from the dorsal body wall. Each is a string of cigar-shaped ovarian follicles of varying sizes, the largest being 5·5 mm long, and the smallest mere specks. Large and small are intermingled irregularly along the length of the ovaries, though the smaller ones are, in general, more dorsally placed than the larger ones.

The right oviduct assumes a somewhat median ventral position in the body cavity for a part of its course. The opening of the oviduct at its very fine, membranous, anterior end is slightly further forward in the body cavity than the anterior end of the right ovary. The degree of convolution of the oviduct varies along its length, being most marked in the central third where it is deeply pleated, and in the region just prior to its entry into the cloaca, where it bends sharply back and forth upon itself many times. On reaching the cloaca, the oviduct becomes very broad and strap-like, and enters the cloaca by a narrow transverse slit in the right dorsolateral region (Fig. 20).

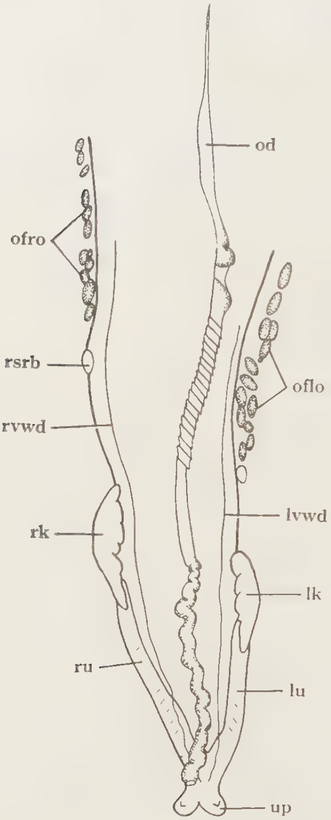


Fig. 16

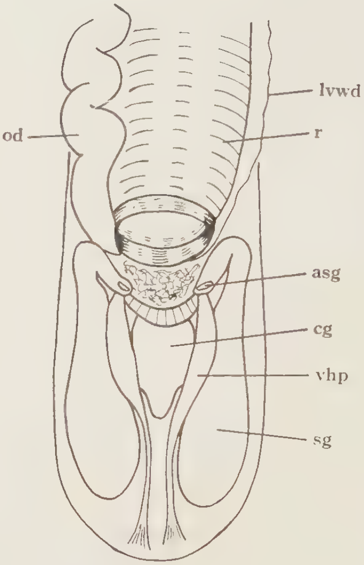


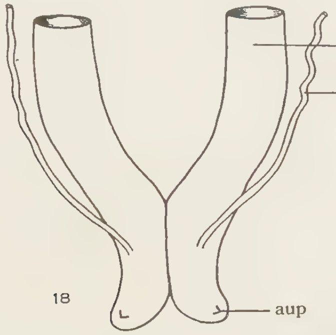
Fig. 17

Fig. 16.—*T. polygrammicus*, renal–reproductive system of female, ventral aspect: *lk*, left kidney; *lu*, left ureter; *lvwd*, left vestigial Wolffian duct; *od*, oviduct; *oflo*, ovarian follicles of left ovary; *ofro*, ovarian follicles of right ovary; *rk*, right kidney; *rsrb*, right suprarenal body; *ru*, right ureter; *rvwd*, right vestigial Wolffian duct; *up*, urinary papilla.

Fig. 17.—*T. australis*, cloacal and postanal regions of female, ventral aspect: *asg*, aperture of scent gland; *cg*, cloacal gland; *r*, rectum; *sg*, scent gland; *vhp*, vestigial hemipenis.

Paired vestigial Wolffian ducts are present in the female, and each appears as a very fine convoluted white duct, arising in the mesentery alongside the corresponding ovary (Fig. 16). The right Wolffian duct lies closely along the dorsal border of the oviduct, and follows the convolutions of the latter faithfully. Just before reaching the cloaca, the Wolffian duct passes on to the mid-ventral surface of the right ureter, and merges with it (Fig. 18).

The left Wolffian duct passes back from the ovary in company with the blood vessels, to the ventral border of the kidney, down which it passes. It then accompanies the renal portal vein to the region of the cloaca, where it merges with the left ureter.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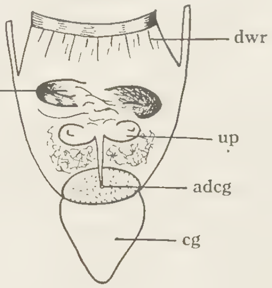
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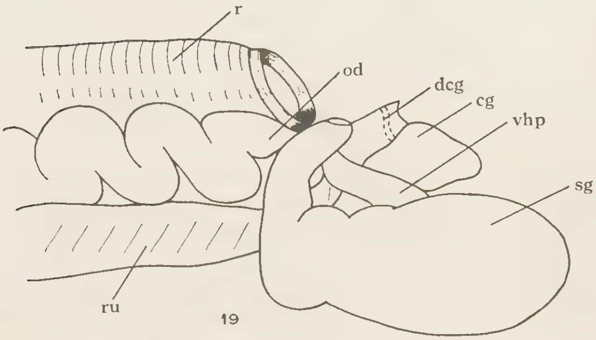
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Fig. 18.—*T. polygrammicus*, terminal region of ureters and vestigial Wolffian ducts: *aup*, aperture of urinary papilla; *lu*, left ureter; *lvwd*, left vestigial Wolffian duct.

Fig. 19.—*T. australis*, cloacal and postanal regions of female, right lateral aspect: *cg*, cloacal gland; *dcg*, duct of cloacal gland; *od*, oviduct; *r*, rectum; *ru*, right ureter; *sg*, scent gland; *vhp*, vestigial hemipenis.

Fig. 20.—*T. australis*, cloaca of female. Dorsal wall of rectum turned forwards: *adcg*, aperture of duct of cloacal gland; *aod*, aperture of oviduct; *dwr*, dorsal wall of rectum; *up*, urinary papilla.

The suprarenal bodies are a pair of small, oval, white or cream-coloured organs, each one lying immediately posterior to the corresponding ovary, and in fact, somewhat resembling an ovarian follicle. It is worthy of note that the two types of tissue of which the suprarenal bodies are composed are both visible as distinct regions—the medullary tissue forming the anterior half of the organ and the cortical tissue the posterior half.

(ii) *The Cloaca*

A wide, tight band of circularly disposed muscle fibres arises from the caudal vertebrae immediately above and behind the cloaca. The band passes ventrally around the body, diverging into two approximately equal parts in the mid-lateral line thus forming the sphincter anae and sphincter caudae. Of these, the former passes ventrally across the rectum immediately in front of the cloaca, and the latter follows the same direction immediately behind the cloaca. There is also a wide longitudinal muscle which lies in the mid-ventral line behind the cloaca—one end is attached to the posterior wall of the cloaca, and the other to the vertebrae in the region of the caudal spine. This muscle tends to pack in between the two scent glands, and round out the ventral contour of the tail.

Although in the cloaca of *Typhlops* the coprodaeum, urodaeum, and proctodaeum do not form three distinct compartments, it has been decided to follow the example of Gadow (1901), and retain these terms in order to facilitate the description of the relevent regions.

The cloaca itself, at first sight, is dominated by the anal aperture (coprodaeum) which is large and rounded, and placed obliquely dorsoventrally in the anterior part of the cloaca. The rectum is thin-walled and very dilated, tapering sharply to the anus. The form of the anus appears to differ specifically; in *T. australis* (Fig. 20) the rectum ends in a wide band of smooth tissue, which projects into the anterior part of the cloacal cavity. This band of tissue is not very thick, but it is moderately rigid (much more so than the wall of the rectum) and it serves to maintain the anus as a wide, circular aperture.

In *T. polygrammicus* the anus has a somewhat different structure. Here the rectum ends in a thickened band of tissue, the inner surface of which is thrown into longitudinal knife-like ridges, and which projects not into the cloaca, but back into the rectum. Its anterior extremity thus forms a ledge or shelf within the rectum. Presumably in this case the tissue is highly muscular and forms a sphincter.

The urodaeum in the female consists of a dorsal portion only, and this is cut off from the rest of the cloacal cavity by the backwardly projecting dorsal wall of the coprodaeum. To examine the urodaeum it is necessary to bend forward this portion of the rectal wall (Fig. 20).

The right oviducal opening is situated in the most anterior part of the urodaeum, immediately above the rectum; a narrow, transverse depression representing the opening of the left oviduct is immediately adjacent. The surrounding tissue has several deep transverse fissures.

Behind the oviducal aperture are the two urinary papillae. These are in mutual contact at their bases in the mid-dorsal line, but each bends outwards, so that the tips, each opening by a V-shaped slit, are laterally directed.

The dorsal wall of the proctodaeum is raised into numerous, irregular projections and folds, with deep grooves between. Francis (1934), in discussing the cloaca of the salamander, suggests that this arrangement may serve the purpose of holding the sperms immediately after copulation.

The scent glands open ventrolaterally into the proctodaeum near its posterior limit. These openings are quite large, and have thick, rather frilled lips (Fig. 17).

The external opening of the cloaca is a small, transverse slit; it is very inconspicuous as it is flush with the skin, and is not surrounded by swollen lips, or by special scales, in either sex.

(iii) *The Postanal Region*

This is a very short region, containing the paired scent glands, the median cloacal gland, and paired vestiges of the male copulatory organs.

(1) *The Scent Glands* (Figs. 17 and 19).—These in the female are much larger than in the male. They lie one on each side of the mid-line and occupy almost all of the caudal region. They are pear-shaped structures, lying with their broadest end posteriorly directed. The gland narrows evenly towards the anterior region, then at the level of the cloaca the neck bends downwards at right angles and enters the cloaca ventrolaterally, behind and below the oviducal aperture.

(2) *The Vestigial Hemipenes* (Fig. 17).—These are paired structures, lying below and between the scent glands. They are very much smaller than their male counterparts, and have no opening into the cloaca. Each consists of an elongate, cylindrical, solid portion, corresponding to the sheath in the male, and a long slender wisp of muscle extending right back to the region of the caudal spine, where it fans out into several fingers which are attached to the caudal vertebrae. Sedgwick (1889) makes the only traceable reference to the presence of vestigial male copulatory organs in female reptiles.

(3) *The Cloacal Gland* (Figs. 17, 19, and 20; Plate 3).—Lying in the mid-ventral line, between and below the vestigial hemipenes, and with its base projecting obliquely forwards along the sloping posterior wall of the cloaca, is a large conical glandular structure. Guibe (1948) describes and figures this in the male only, but in the specimens dissected in the current work, it was equally well developed in both sexes.

The structure is made up of a large number of coiled, tubular glands, the products of which drain into a central longitudinal canal (Plate 3). This canal bends sharply downwards at the anterior end of the gland, pierces the dorsal cloacal wall, and opens mid-dorsally into the proctodaeum by a very small aperture at the tip of a longitudinal fold.

Guibe homologizes this structure with the "dorsal gland" of lizards—to which no other reference can be found. Francis (1934) describes the cloaca of the male salamander as being "surrounded by a large tubular gland", but says that this gland is absent in the female. He describes the gland as being divisible into three portions, the pelvic gland, the abdominal gland, and the cloacal gland. The latter he describes as "a heart-shaped structure surrounding the cloacal opening, and is seen to consist of a mass of coarse tubules. It discharges its secretion by numerous fine pores situated at the extremities of the long papillae arranged in the (ventrolateral) cloacal walls." Regarding the function of these glands Francis states "[It] is to secrete mucoid spermatophores which envelop the sperms when they are shed by the male in copulation." The same author also points out that some earlier workers have tried to homologize these glands with the prostate of mammals, but while recognizing that there is some functional similarity, doubts the actual homology.

As regards the function of the gland in *Typhlops* it is possible that its secretion may serve the purpose of assisting both the transfer of the sperm from the male, and its reception into the cloaca of the female.

(*b*) *Male* (Figs. 21–24)

(i) *The Right Testis, Suprarenal Body, and Kidney*

These are all larger and further forward in the body cavity than are the corresponding organs on the left (Fig. 21). Also the right vas deferens is longer and more convoluted in the region between the adrenal and the kidney, than is the case on the left.

The kidneys, suprarenal bodies, and the ureters for the greater part of their length, are as described for the female. As in the female, the ureters become joined by their mesial walls, just anterior to the cloaca, though again their ducts do not become confluent. In the male, however, the ureters do not open into the cloaca through urinary papillae, but directly, and right in the anterior dorsal region of the urodaeum–in much the same relative position as the oviduct opens into the female cloaca (Figs. 21 and 22).

Each testis is a white, compact organ, rather crescent-shaped, with the concave edge directed towards the mid-line of the body. The posterior tip is quite a distinct lobe. The testes are suspended from the dorsal wall of the body cavity by the mesorchium, a short distance in front of the kidneys. Each testis is drained by a stout vas deferens, which is closely applied to the inner border of the testis, and projects slightly forward of the anterior end. The vas deferens is connected to the testis by a number of very fine vasa efferentia. The vas deferens leaves the testis at the posterior tip and passes back through the body cavity, closely bound to the postcaval vein and to the suprarenal body, to the dorsal surface of which it is closely applied. Still in association with the vein, it passes to the anterior tip of the kidney.

In the case of the right vas deferens, there is marked convolution and some local dilation, before the duct passes on to the inner surface of the kidney, and becomes associated with the ureter, with which it leaves the posterior tip of the kidney. It passes along the outer border of the ureter for the greater part of the distance between the kidney and the cloaca, but just before the two ureters become joined, the vasa deferentia bend fairly sharply downwards and inwards, and each appears to enter the corresponding ureter ventrally. However, a more detailed investigation shows that although each vas deferens does pass into the ureter of the same side, yet the genital and urinary ducts remain separate. There are thus four closely associated apertures opening into the anterior dorsal region of the urodaeum. At this stage the vasa deferentia appear as small cylindrical tubes lying on the ventral floor of the ureters (Fig. 22).

(ii) *The Cloaca*

The coprodaeum does not call for any further comment than the description given for the female. The urodaeum, again consisting mainly of the dorsal portion, has in its most anterior extremity, the apertures of the urinary and genital ducts described above.

Posterior to these openings, and in the mid-dorsal wall of the proctodaeum, are the confluent openings of a pair of structures which were at first sight taken to be the hemipenes. Further investigation, however, revealed that this was not so. Guibe (1948) describes these organs in *Typhlops*, and gives them the title of "retro-cloacal formations", but does not suggest what their specific function might be. He hints that for him they recall the rectal gland of the selachians, but does not expand on this somewhat mystifying suggestion.

These retro-cloacal formations, then, are a pair of elongate, hollow structures, like blind caecae, lying one on each side of the body cavity, in the dorsolateral aspect, and they appear to vary specifically. In *T. polygrammicus* (Fig. 21) they are stiff, rod-like structures, much longer and thinner than in *T. ligatus*, and they project directly forwards in the dorsolateral aspect of the body cavity. In *T. ligatus* (Fig. 22) they are rather soft, stout, pouch-like structures, which bend obliquely forwards and downwards, tending to become wrapped around the lateral walls of the rectum. In both cases, the walls of these structures are thick and muscular, and the cavity within them very narrow. They do not possess any muscular attachments.

The dorsal and lateral walls of the cloaca in the male are thrown into fairly steep, knife-like, longitudinal ridges, which are particularly pronounced in the region of the urodaeum.

As in the female, the external aperture of the cloaca is very inconspicuous. Unlike many male reptiles, the cloacal aperture of *Typhlops* is not bounded by fleshy lips.

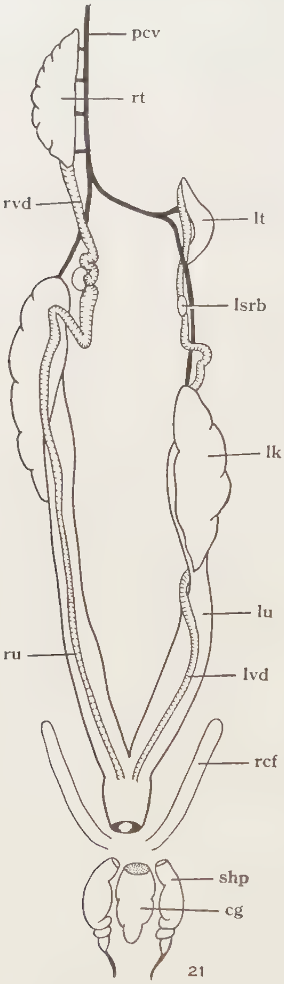
(iii) *The Postanal Region*

The scent glands are much smaller than they are in the female, but are of the same shape and disposition (Fig. 22). The ducts are similar and open into the same region of the cloaca as in the female.

The cloacal gland (Figs. 21 and 22) is of the same proportions, and opens into the cloaca in the same manner, as in the female.

The Hemipenes (Figs. 21, 22, and 24).—Just behind the apertures of the scent glands, and at the posterolateral corners of the cloaca are a pair of apertures, each of which leads back into a cylindrical sheath of connective tissue (Fig. 22). This sheath at first dilates fairly regularly as it passes back, reaching its maximum distention about two-thirds of the way along its length. Thereafter its diameter diminishes quite rapidly and it becomes spirally twisted through one and a half turns. The sheath is of approximately the same length as the scent gland.

Contained coiled up within this sheath is the hemipenis (Fig. 24*B*), a very long, thin tubular structure, which can be protruded through the aperture into the cloaca, and in one specimen was found to be extended through the external cloacal aperture to the outside of the body. The protruded portion was approximately 10 mm in length. The hemipenis passes right through the length of the sheath, and continues on to the posterior limit of the body, where it ends in a fan-shaped arrangement of muscles which are attached to the body wall in the region of the caudal spine (Fig. 24*A*).



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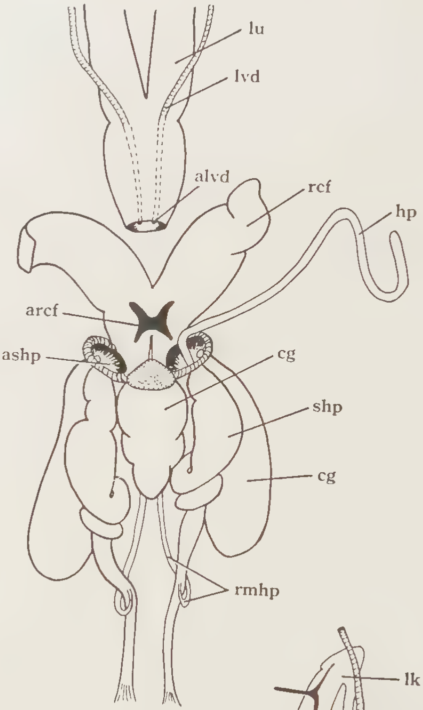

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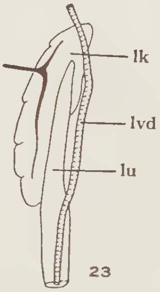

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Fig. 21.—*T. polygrammicus*, renal-reproductive system of male, ventral aspect: *cg*, cloacal gland; *lk*, left kidney; *lsrb*, left suprarenal body; *lt*, left testis; *lu*, left ureter; *lvd*, left vas deferens; *pcv*, postcaval vein; *rcf*, retrocloacal formations; *rk*, right kidney; *rt*, right testis; *ru*, right ureter; *rvd*, right vas deferens; *shp*, sheath of hemipenis.

Fig. 22.—*T. ligatus*, cloacal and postanal region of male, ventral aspect: *alvd*, aperture of left vas deferens; *arcf*, aperture of retrocloacal formations; *ashp*, aperture of sheath of hemipenis; *hp*, hemipenis; *rmhp*, retractor muscle of hemipenis.

Fig. 23.—Dorsal surface of left kidney: *lk*, left kidney; *lu*, left ureter; *lvd*, left vas deferens.

At its posterior end, the sheath becomes fairly loosely attached to the hemipenis, and somewhat inverted within its own cavity. This is, of course, especially the case when the hemipenis is protruded into and beyond the cloaca.

A pair of long slender muscles arises from the posterior wall of the cloaca, one on each side of the mid-line of the body, and just above the cloacal gland. These muscles pass backwards, above and between the sheaths of the hemipenes, until they reach a point approximately half way between the end of the sheaths and the posterior limit of the body cavity. Here each muscle bends downwards on the outer side of the hemipenis, then turns sharply forwards and its fibres become merged into the tissue of the hemipenis, finally coming to occupy a central position in it (Fig. 24*A*, *D–G*).

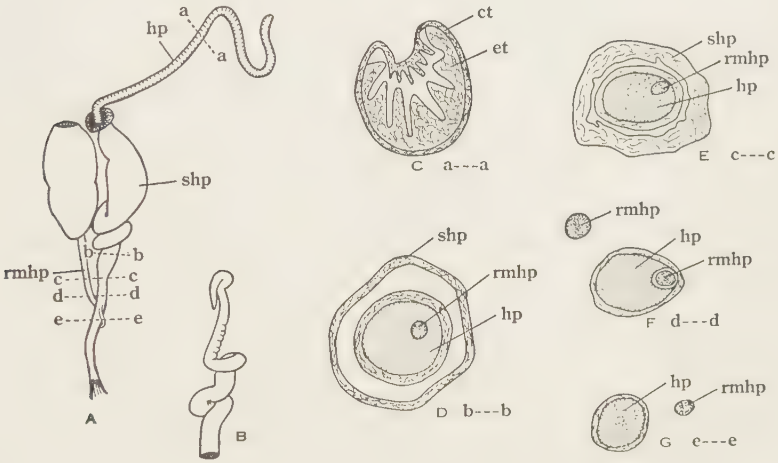

Fig. 24.—Hemipenis: *A*, hemipenis extruded from sheath. *B*, retracted hemipenis removed from sheath. *C–G*, sections as indicated: *ct*, connective tissue; *et*, erectile tissue; *hp*, hemipenis; *rmhp*, retractor muscle of hemipenis; *shp*, sheath of hemipenis.

Histologically, the hemipenis shows considerable variation along its length (Fig. 24*A*, *C–G*). The protrusible portion is composed of what appears to be erectile tissue. It is bound externally by a layer of connective tissue, and is grooved along one surface. Inside the connective tissue is a horseshoe-shaped area of erectile tissue which is thrown into a series of longitudinal folds, the tops of which are directed towards the groove. Between the groove and the tops of the folds is a space, which is of course continued in fingers between the folds. The connective tissue lining the groove sends several projections into this space—the number of connective tissue projections being approximately equal to the number of indentations between the ridges. This arrangement would give extra rigidity when the tissue was functional. Externally, the hemipenis is quite smooth, lacking any trace of spines or ridges. It is not bifid at its free end, but when retracted within the sheath, the tip of the hemipenis is bent right over on itself, like the handle of a crook.

More posteriorly, within the sheath, the hemipenis becomes muscular, and the fibres of the retractor muscle can be seen as a separate bundle towards its centre. Although there is only one oviduct in the female, the two hemipenes of the male are equally well developed.

The hemipenis of *Typhlops* is unlike that of any snake or lizard of which a description can be found. It certainly does not fit into any of the generalized descriptions of the copulatory organs of the Ophidia given in standard textbooks of zoology. Sedgwick's (1889) description reads, "The males always possess external organs of copulation, ... In Snakes and Lizards these organs consist of two protrusible hollow tubes, which are either smooth or covered with spines and lie retracted in a pouch-like cavity behind the cloaca. When protruded their surface is traversed by a groove which conveys the sperm from the genital openings of the cloaca."

Gadow (1901) states, "The cloacal arrangement [of snakes] is essentially the same as that of the Lacertilia, but snakes possess no urinary bladder. The copulatory organs are stowed away beneath the skin in recesses of the posterior lateral corners of the shallow cloacal vestibulum. Each organ is usually bifurcated at the free end, and furnished with little spike-shaped, but scarcely horny, excrescences."

Two recent workers, Smith (1943) and Guibe (1948), have described the reproductive organs of *Typhlops*, but the former seems to have mistaken the hemipenial sheath for the copulatory organ, for he says, "The hemipenis of *Typhlops diardi* . . . . . is short and fat, with convoluted plicae; there are no spines." Guibe refers to "the sheath of the hempenis", but does not mention the hemipenis itself.

McCann (1946) describes the hemipenis of snakes and lizards, when everted, as presenting the shape of a flower bud with a short or long stalk, the "bud" or head frequently being armed with spines; or fleshy collars, or ridges; or possessing horn-like appendages. He suggests that the structure and position of the organ indicates that it is used not only to assist in the transfer of sperms from the male to the female, but also to establish a firm copulatory hold within the female during mating. It is difficult to imagine that the long, slender hemipenis of *Typhlops* functions in this way.

Some reptilian groups, e.g. the crocodiles and chelonians, have a single median penis, which is solid, and grooved along the supper surface. Smith (1943) describes it thus: "It arises from the ventral wall of the proctodaeum, and is extended through the anterior end of the cloacal slit." It is to be noted that the organ is retracted within the cloaca while in the resting position; it is not invaginated. Hence, in that it is solid, and externally grooved, and is retracted into the resting position, each hemipenis of *Typhlops* bears a greater superficial resemblance to the single penis of the crocodiles and chelonians, than to the hemipenis of other snakes.

VI. Discussion

The results of this work show that there is still a great deal to be learnt from the anatomy of members of this and related genera, concerning their phylogenetic and taxonomic relationships. It is clear that *Typhlops* cannot be classified as an ophidian, since there are points of dissimilarity of structure between this genus and the snakes, in every system examined. Some of these dissimilarities are small, and considered individually, insignificant; others, such as the structure of the hemipenis, the clocal gland, the "retro-cloacal formations", the anomalous respiratory system, and the lobulated liver have far-reaching implications.

At the moment it is only possible to make negative suggestions. Further work is planned on other genera of "blind snakes", in an attempt to establish more positively their true taxonomic position.

VII. Acknowledgments

The author is greatly indebted to Professor W. R. McGregor, Head of the Department of Zoology, University of Auckland; Mr. J. M. de Bavay, Department of Zoology, University of New England, and Mr. F. J. Mitchell, South Australian Museum, for assistance in obtaining specimens.

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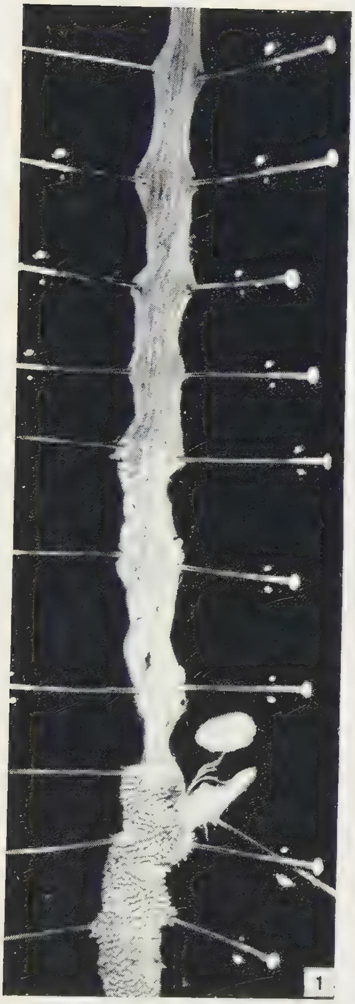
PLATE 1



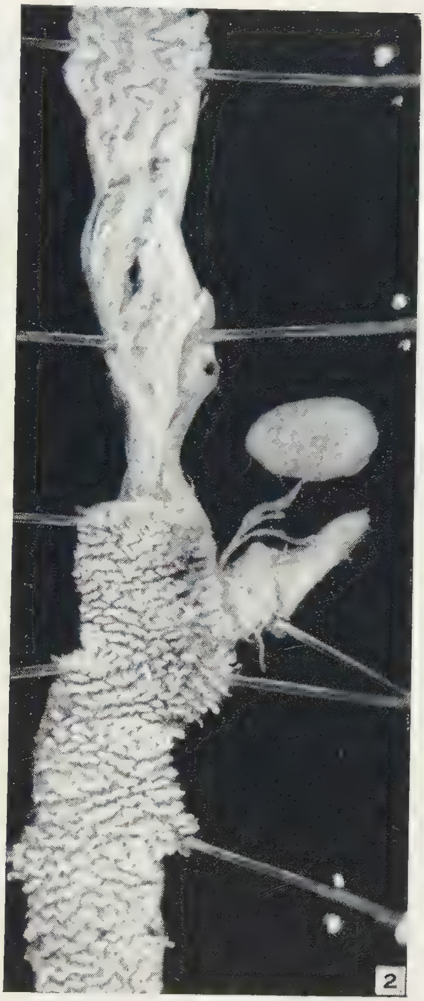
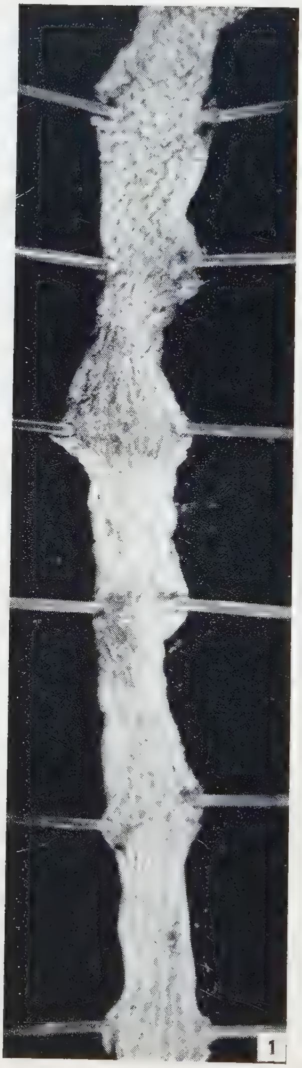


Fig. 1.—Internal lining of oesophagus (upper), stomach (centre), and duodenum (lower) of *Typhlops ligatus*. Gall bladder, pancreas, and spleen also shown.

Fig. 2.—Internal lining of cardiac and pyloric regions of stomach and of duodenum. Gall bladder, pancreas, and spleen are shown, and the point of entry into the duodenum of the bile and pancreatic ducts is visible.



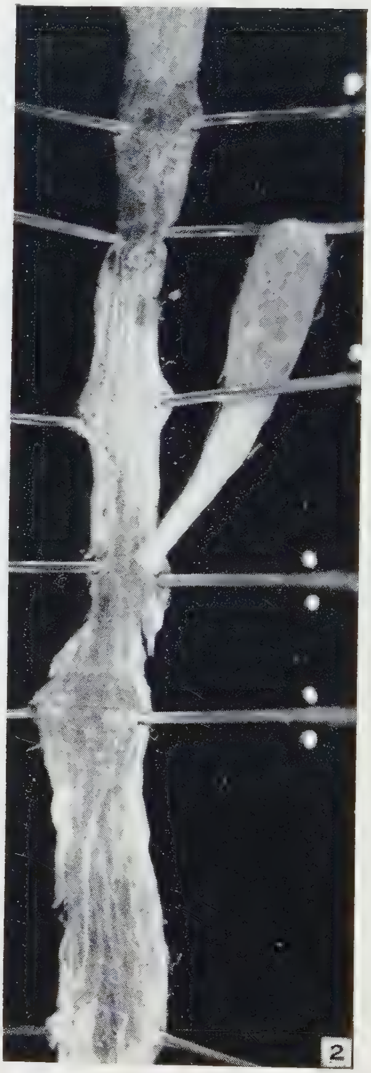
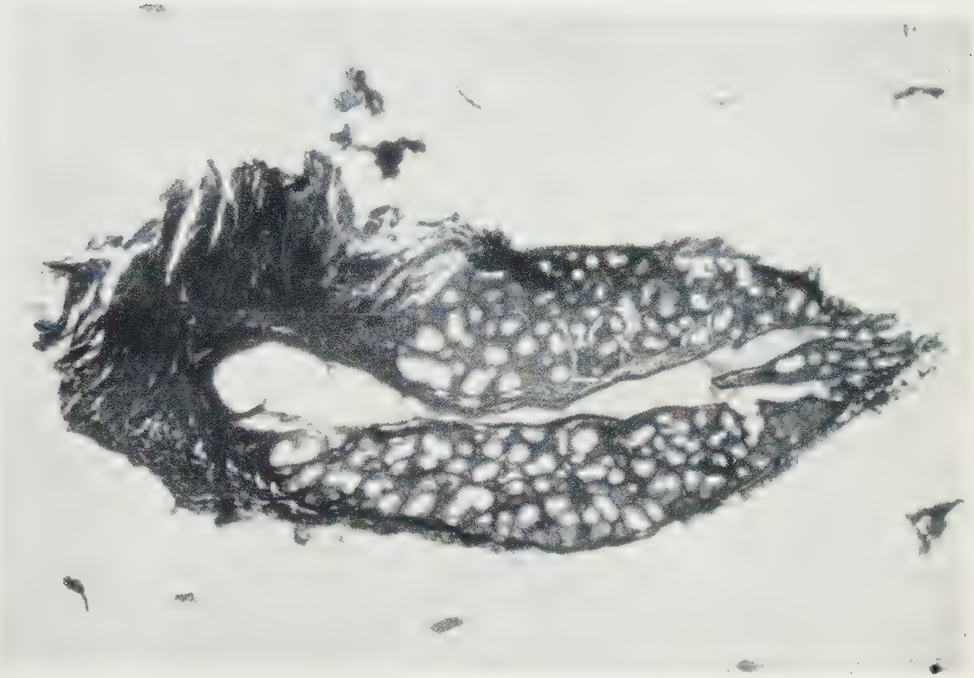


Fig. 1.—Internal lining of posterior region of intestine, showing gradual change in structure from villi to ridging.

Fig. 2.—Internal lining of posterior region of intestine and rectum. The caecum is shown on the right.



Longitudinal vertical section of cloacal gland of *Typhlops*.

LIFE HISTORY OF *ACANTHOPARYPHIUM SPINULOSUM* JOHNSTON, 1917 (TREMATODA: ECHINOSTOMATIDAE)

By A. J. Bearup*

[*Manuscript received November* 24, 1959]

Summary

A list is given of the trematode cercariae which are commonly found in the estuarine gastropod, *Pyrazus australis*† Quoy & Gaimard. These include: cercariae of a schistosome, *Austrobilharzia terrigalensis* Johnston, 1917, and of a heterophyid, *Stictodora* sp.; a monostomate xiphidiocercaria, probably belonging to the Microphallidae; two megalurous cercariae, probably belonging to the Philophthalmidae; and one echinostome cercaria. The life history of the latter, *Acanthoparyphium spinulosum* Johnston, 1917, is described.

No sporocysts were found. Two generations of rediae precede the cercariae, which have a collar with 23 spines in a single row, as in the adult.

Cercariae encyst readily in *Salinator fragilis* (Lamarck), another gastropod living in the same habitat. Cysts were also found occasionally in *P. australis* and in small polychaetes of the *Phanaerocephala* group. Adults were obtained by feeding *S. fragilis*, which contained encysted cercariae, to the silver gull, *Larus novaehollandiae*.

I. Introduction

This paper is part of a study of the trematode parasites of snails living on estuarine sandflats in the Sydney district. Recent investigations (Bearup 1955, 1956) of "bather's itch" in these localities indicated that the schistosome cercaria *Austrobilharzia terrigalensis* Johnston, 1917, was the probable cause. These cercariae were found only in the gastropod *Pyrazus australis*† Quoy & Gaimard, which commonly occurs in association with eel grass (*Zostera* sp.) in estuaries and coastal lagoons on the eastern coast of New South Wales.

The study of schistosome dermatitis required the examination of large numbers of *P. australis* and as a result other types of trematode cercariae were found to be commonly associated with this gastropod. These include a pleurolophocercous cercaria belonging to the genus *Stictodora* (Heterophyidae), a monostomate xiphidiocercaria probably belonging to the Microphallidae, two types of megalurous cercariae probably belonging to the Philophthalmidae (probably *Cloacitrema*), and one echinostome cercaria, *Acanthoparyphium spinulosum*, Johnston, 1917. The life history of *A. spinulosum* is described.

Acanthoparyphium infection rates in *P. australis* rise to a maximum in summer and fall to a minimum in late winter. A seasonal rise and fall has occurred in five successive years from 1954 to 1958; the fluctuations in one year are shown in Table 1.

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† *Pyrazus australis* is now usually placed in the genus *Velacumantus* Iredale—see *Rec. Aust. Mus.* **19**: 292 (1936).

Summer maxima have been 21, 15, 3·5, 20, and 33 per cent. in the five years and the overall infection rate about 11 per cent. in 4000 *P. australis* examined. Double and triple infections with other cercariae are often found. Only one infection with *Acanthoparyphium* cercariae has been found in a mollusc other than *P. australis*; this was in *Salinator fragilis* (Lamarck). The names and numbers of molluscs examined from the same habitat are as follows: *Pyrazus ebeninus* Brugiere (66); *Austrocochlea obtusa* Dillwyn (36); *Parcanassa ellana* Iredale (79); *Austropyrgus ruppei* Hedley (1023); *S. fragilis* (359).

Table 1

VARIATIONS IN ONE YEAR OF THE INCIDENCE OF ACANTHOPARYPHIUM CERCARIAE IN P. AUSTRALIS AND THE CHLORIDE CONTENT OF NARRABEEN LAGOON WATER

Date	20.xii.57	22.i.58	26.ii.58	23.iii.58	4.v.58	11.vi.58	3.ix.58	8.x.58	21.xi.58	5.i.59
No. of cercariae (%)	20	17	20	18	8	5	9	9	33	11
Chloride (%)	1·46	1·07	0·89	1·84*	1·52	1·59	1·52	1·22	1·37	1·18

* Lagoon open to sea.

II. History of the Genus Acanthoparyphium

The genus *Acanthoparyphium* was created by Dietz (1910) with the single species *A. phoenicopteri* (Luhe, 1898) from a flamingo, *Phoenicopterus roseus*, in North Africa. All new species added to the genus have come from localities on the eastern shores of the Pacific Ocean. Johnston (1917) described *A. spinulosum* from a plover, *Charadrius dominicus*, from Sydney; Tubangui (1933) followed with *A. ochthodromi* from another plover, *Octhodromus mongolus*, in the Philippine Is. Yamaguti (1958) lists nine species and one subspecies, seven of them described by him from material collected in Japan.

Skryabin (1956) gives a key to eight species in the genus; the main points for separation are the extent of the yolk glands and the position of the testes. He omits one each of Yamaguti's species and subspecies: *A. tyosenense* Yamaguti, 1939, as a synonym of *A. kurogamo* Yamaguti, 1939, and *A. spinulosum suzugamo* Yamaguti, 1939, as a synonym of *A. spinulosum*. The subspecies was distinguished only by the smaller size ratio of oral sucker and acetabulum (2·8 as against 3·5 to 1); in eight specimens from the author's experimental feeding (fixed and not under compression) the ratios were 2·6, 2·6, 2·8, 2·8, 3·0, 3·1, 3·3, and 3·4 to 1, so that the subspecies seems to have no standing.

Hosts of *Acanthoparyphium* are always aquatic birds and most of them are migratory; some of them, like plovers, godwits, knots, and dotterels fly from Siberia to southern Australia so that eggs of species other than *A. spinulosum* must often be brought into this country. Specific differences in the cercariae are not yet known and it is possible the values given in Table 1 include infections of more than one species. Some species previously recorded only in Japan were recently found by the author in migratory birds in north Queensland. The parasites and their hosts are: *A. marilae** Yamaguti, 1934, in the godwit, *Limosa lapponica*, and in the knots, *Calidris tenuirostra* and *C. canuta*; *A. squatarolae** Yamaguti, 1934, in *C. tenuirostra*, and *L. lapponica*. At the same time and place *A. spinulosum* was found in a dotterel, *Charadrius leschenaultii*. Other hosts of this parasite are those recorded by Yamaguti (1934, 1939) in Japan, namely a plover, *Squatarola hypomelaena*, and a duck, *Nyroca mariloides*.

III. Stages in the Life Cycle of A. spinulosum

(a) *Habitat*

The snails used in this study were obtained from a sandflat in Narrabeen Lagoon, an estuary located 16 miles north of Sydney. A narrow channel at one end connects the estuary with the sea, but it is often blocked with sand which is not removed until after heavy rain. The chloride contents of the lagoon water over the sandflat (estimated as g/100 ml) varied from 0·7 after heavy rain to 1·6 in a dry spell when the lagoon entrance was blocked; when it was open to the sea the value was 1·84 which is close to that of sea-water (1·9). Ten of these estimations, covering a period of 12 months, are included in Table 1.

(b) *Methods*

Collections of *P. australis* were made at about monthly intervals. The snails were stored in a refrigerator in screw-top jars. About 200 were crushed to establish the incidence of cercarial types; others were kept in a small amount of lagoon water in 4 by 1 in. glass tubes to get naturally emerging cercariae.

Live rediae and cercariae were examined in horse serum diluted with Ringer's solution which was sometimes lightly coloured with neutral red. Other rediae and cercariae were killed and preserved by Talbot's (1936) method.

Encysted cercariae (metacercariae) were obtained experimentally by placing the small, thin-shelled gastropod *S. fragilis* in lagoon water containing naturally emerged cercariae. These snails were fed to young gulls, *Larus novae-hollandiae*, which had been fed only on beef heart since their capture as fledglings. Adults were subsequently recovered from the gull's small intestine.

(c) *Ovum* (Fig. 9)

Eggs from the faeces of the experimental gull and in the uteri of preserved adults measured 0·092–0·100 by 0·065–0·076 mm. Those from the faeces were oval-shaped, colourless, thin-shelled, with a smooth outline, and filled with yolk cells. They were few in number, insufficient for infecting the snail host. Adults kept in saline for 24 hr did not lay any eggs. Eggs dissected from the uterus were kept in saline for 45 days at summer room temperature (25–30°C) but by then had degenerated without developing miracidia.

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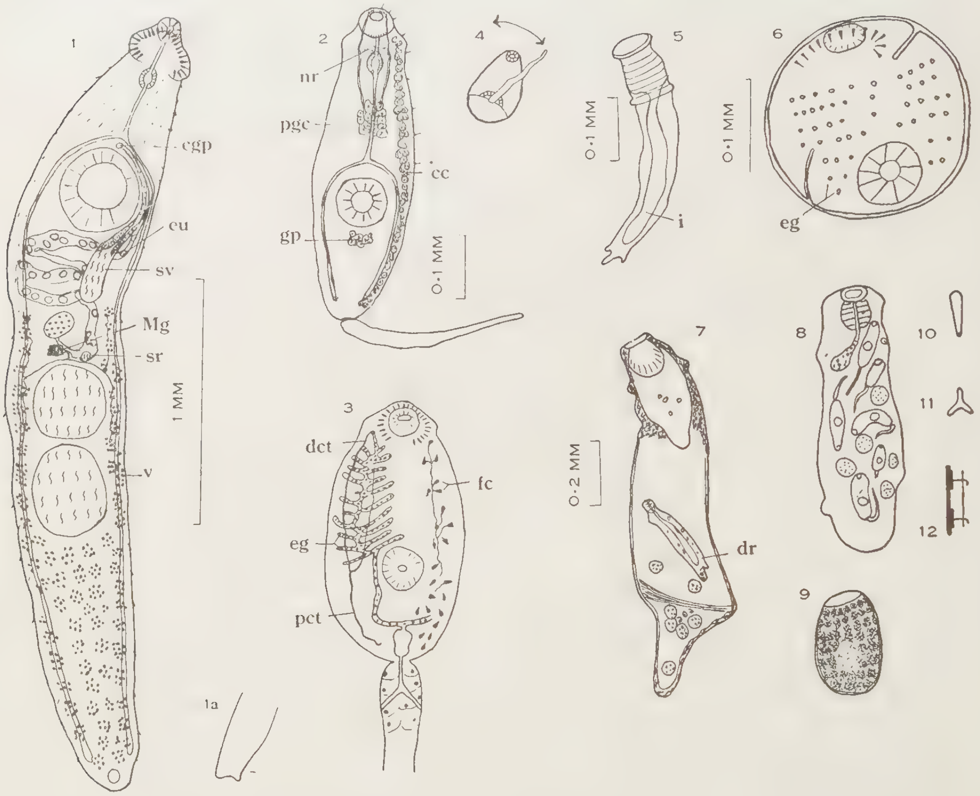
* The diagnosis of these two species is given with the reservation that the author thinks they might be identical and that the differences in the extent of the yolk follicles which characterize them represent different stages of maturity. Both species were present together in six out of eight birds with *Acanthoparyphium* infections, the others were one each of *A. marilae* and *A. spinulosum*.



Figs. 1–12.—Stages in the life cycle of *A. spinulosum*: 1, mature adult; 1*a*, adult, posterior end bifurcate; 2, cercaria, cystogenous cells shown on left side only; 3, cercaria, excretory system; 4, cercaria, swimming position; 5, redia, early stage; 6, metacercaria, encysted; 7, redia with developing daughter redia; 8, redia with developing cercariae; 9, ovum; 10, collar spine 11, spine from cirrus; 12, body spines. Figures 1, 2, 5, 6, and 7 drawn with aid of projector. *cc*, Cystogenous cells; *cgp*, common genital pore; *dct*, descending collecting tube; *dr*, daughter redia; *eu*, egg in uterus; *eg*, excretory granules in lateral caeca; *fc*, flame cells; *gp*, genital primordium; *i*, intestine; *Mg*, Mehlis gland; *nr*, nerve ring; *pct*, posterior collecting tube; *pgc*, penetration gland cells; *sr*, seminal receptacle; *sv*, seminal vesicle; *v*, vitelline glands.

(*d*) *Redia* (Figs. 5, 7, and 8)

No sporocysts were found. Early larval stages were present in gill filaments and in tissues surrounding the mantle of the snail host. Rediae were colourless, and had a mouth cavity, a pharynx as wide as the body, and a gut extending into the posterior half of the body. The smallest ones had no collar or foot processes and measured 0·15 mm in length; later stages from the same tissues of the host were up to 0·48 mm in length, and had well-developed collars and foot processes and free germ balls in the body cavity.

The host digestive gland contained a few colourless rediae like those in the mantle but these were greatly outnumbered by larger yellowish rediae up to 1·6 mm in length. The latter contain germ balls and immature and mature cercariae. Pigment occurs all over the body, except the anterior tip, as coloured granules in the outer edges of the body wall. The collar and foot processes disappear in rediae greatly distended with cercariae; the gut is relatively smaller in these larger rediae and is confined in a small space just behind the pharynx. No birth pore could be identified with certainty and no cercaria was ever seen to escape from any redia.

One colourless redia was found with a daughter redia developing inside it (Fig. 7), otherwise the rediae contained cercariae or larvae too young to be identified.

(*e*) *Cercaria* (Figs. 2, 3, and 4)

The cercaria can be distinguished under low magnification by the large number of excretory granules in the two main ascending excretory ducts and in the extensive system of lateral caeca attached to them (Fig. 3). They are very active (sometimes they will swim about for 30 sec but usually for about 10 sec, without a stop) and the swimming position is with the anterior and posterior ends brought together in U-shape. From the dorsoventral view the body is then rounded. The projecting tail moves laterally (Fig. 4) with powerful strokes and drags the body behind it. Although very active the cercariae do not gain much height and most of them remain near the bottom of the container. They creep over surfaces by the alternate use of their oral and ventral suckers. When newly emerged they show a marked attraction towards daylight and move quickly towards the lighted side of the dish.

The mean measurements of 10 cercariae freshly killed in hot formalin were: body length and breadth, 0·404 by 0·175 mm; tail length and breadth, 0·261 by 0·039 mm at the base; oral sucker diameter, 0·021 mm; acetabulum, 0·049 mm; pharynx 0·026 by 0·022 mm.

The cuticle is marked by fine ridges in parallel transverse rows. Just below the level of the oral sucker there is a definite shoulder which carries a single row of 23 spines without any special grouping of corner spines. In dilute neutral red the cuticular bristles are more prominent and nine bristles, set in papilliform bases, were found along each lateral border. At the head end and ventral to the first row is a second one of five smaller pairs, apparently without papilliform bases.

The suckers are rounded; the oral sucker is slightly smaller than the ventral sucker, which is near the junction of the middle and posterior thirds of the body. The mouth is subterminal and ventral and opens into the oral sucker. There is a short pre-pharynx and a long post-pharynx which divides just anterior to the acetabulum. The narrow caeca extend nearly to the posterior end. A nerve ring encircles the base of the pre-pharynx, and laterally it gives off prominent anterior and posterior main nerve trunks.

A group of gland cells centrally placed between the two suckers is connected by two ducts of unequal size on each side which open at the anterior border of the oral sucker. The number of cells is small: in immature cercariae six were counted and in mature cercariae they are obscured by the excretory granules. Cystogenous cells filled with refractile rods lie just beneath the surface all over the body except for short spaces at each end. Two rounded groups of cells posterior to the acetabulum are taken to represent testes in the genital primordium.

The excretory vesicle is thin-walled. Anteriorly, a short duct divides into two ascending collecting tubes which run dorsally to a position just anterior to the acetabulum, where they develop 10–14 lateral caeca on both sides. The ascending tubes and the caeca are filled with refractile, rounded granules of *c.* 0·005 mm diameter. The main ascending tubes go forward to the level of the oral sucker, then return as main descending tubes to the acetabulum where they divide into anterior and posterior collecting tubes. Up to 24 flame cells were counted on one side of the body but some of them are always hidden by the excretory granules and no satisfactory count was ever made. A short duct from the excretory vesicle into the tail divides into two branches which open laterally.

Cercariae become motionless when transferred to fresh water (0·06 per cent. chloride) and die within an hour; in brackish water (0·3–1·55 per cent. chloride) they will remain alive for 3 days in cool weather.

(*f*) *Metacercaria* (Fig. 6)

Metacercariae are coiled in thin-walled oval or rounded cysts 0·18–0·20 mm in diameter, with the characteristic caeca of the excretory tubules well marked by granules, and with both suckers plainly visible. The size increases little with age but minor changes occur in the larva. It becomes clearer by loss of granules and the collar spines are more prominent.

S. fragilis, 11 days after exposure to freshly emerged cercariae, were fed to a young gull, *Larus novae-hollandiae*, and 14 days later trematode eggs were present in the bird's faeces. The gull was then killed and 30 mature *A. spinulosum* adults were found in the small intestine, mostly in the first 15 cm. A domestic duck and a pigeon were also fed *S. fragilis* containing cysts but no adults were found post-mortem.

Metacercariae are rarely found in *P. australis* but in summer up to 10 per cent. *S. fragilis* living on the same sandflat were found to carry a natural infection and under experimental conditions cercariae readily encysted in this mollusc. The cysts were usually in the foot, sometimes in the mantle, or on the operculum. Occasionally metacercariae were found in the sediment at the bottom of the tubes holding the snails and probably they form free cysts when no suitable gastropod host is available.

No metacercarial cysts were found in small fish or in prawns associated with *P. australis* in the weed beds nor did the cercariae encyst in them when given the opportunity. However, two small polychaetes of the *Phanaerocephala* group were attacked by cercariae and several were seen to penetrate into the body cavity; in a few hours 25 had encysted in the body cavity of one worm.

(*g*) *Adult* (Fig. 1)

Ten adults were examined in detail: one living specimen, five fixed in Bouin's solution and cleared in creosote, and four stained with acid carmine. They agreed closely with Johnston's (1917) description and with the type slide of *A. spinulosum.* The body size of one living specimen, relaxed and under slight coverslip pressure, was 5·75 by 0·95 mm; that of five fixed specimens varied from 4·2 to 5·25 mm (av. 4·7 mm) by 0·60 to 0·75 mm (av. 0·70 mm). These compare favourably with Johnston's measurements of 5·55 by 0·8 mm. A further shrinkage of 10 per cent. occurred when adults were stained and mounted in Canada balsam.

In preserved material the body takes a sharp ventral bend at the acetabulum and, in some specimens, a dorsal bend at the oral sucker. The posterior end has a bifurcation in some cases, which gives two equal and bluntly rounded ends, and these are present in the type specimens also (Fig. 1*a*). Cuticular spines, pointing backwards (Fig. 12) cover the anterior body surfaces to the level of the acetabulum. On the ventral side they continue in decreasing numbers to the posterior end.

The oral sucker is 0·15–0·18 by 0·18 mm; the acetabulum is globular and protrusible and measures 0·44–0·50 by 0·47–0·52 mm. Ratios between the two in eight fixed specimens were 2·6, 2·6, 2·8, 2·8, 3·0, 3·1, 3·3, 3·4 (3·5 according to Johnston), and in the living adult examined, 3·8. The mid-point of the acetabulum is at about one-fifth of the body length from the head end. The collar width (0·3 mm) is about half the body width (0·60–0·77 mm). The wedge-shaped collar spines are 0·067–0·089 by 0·018 mm (0·075 by 0·016 mm according to Johnston) with the innermost ventral pair the smallest. There are 23 in a single row without any special corner groups.

The seminal vesicle extends nearly to the level of the ovary. Anteriorly it is constricted to a narrow tube which widens again as it joins the cirrus. A group of prostate cells surrounds the constriction. Triradiate spines on the cirrus (Fig. 11) are easy to see in living specimens but are almost invisible after preservation in Bouin's fixative. Male and female ducts run forward side by side around the dorsal side of the acetabulum and join at the common genital pore.

The uterus near the ovary contains a large mass of sperm and evidently acts as a receptaculum seminis uterinum. The uterus is confined to the space between the testes and the acetabulum and contains only a few (*c.* 30–50) eggs.

The excretory pore is subterminal on the ventral side and a short duct joins it to the excretory vesicle. Two main ducts pass anterolaterally around the acetabulum; in front of this they develop numerous lateral caeca on each side. The granules in these caeca obscure the details of the smaller ducts and of the flame cells.

The type slide of *A. spinulosum*, W428 in the Australian Museum, Sydney, consists of three pieces: one anterior portion from the head to the posterior testis and two similar posterior pieces containing only yolk follicles. Additional specimens from my own experimental material have now been deposited in the Australian Museum as homotypes: W3682 and W3683 are stained and mounted on slides and W3684 is in glycerine alcohol. Other specimens are stored in the Museum of the School of Public Health and Tropical Medicine, Sydney, labelled Mn1383.

IV. Discussion

The life cycle of *A. spinulosum* is similar to that of most other echinostomes. The difficulties of finding sporocysts and of separating mother and daughter rediae seem to be usual in this group and Stunkard (1938), working on the closely related *Himasthla quissetensis*, could not find mother rediae until he studied sectioned material. He noted that the numbers and arrangement of nuclei are different in the pharynx of a redia and in the oral sucker of a cercaria, also that the enclosed daughter redia could be identified by the presence of foot processes and pharynx, and by the absence of oral sucker and acetabulum.

Larval stages of *Acanthoparyphium* have previously been noticed in Japan. Yamaguti (1934) described a redia and cercaria from *Batillaria multiformis* and said that the metacercariae were found free in the liver or in redia in the same snail. Ito (1957) described a redia and cercaria of this genus from three snails from brackish water—*Tympanotus microptera*, *Cerithidea cingulata*, and *C. largillierti*. Metacercariae were said to occur in the mussel *Laternula kamakurana* but attempts by him to infect it experimentally did not succeed. The rediae and cercariae described by both authors show no distinguishing features from similar stages of *A. spinulosum.*

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THE HAEMATOZOA OF AUSTRALIAN BIRDS

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Summary

Four species of trypanosomes have been described from birds, *Trypanosoma myzanthae* from *Myzantha melanocephala* being new. Several other possibly distinct species are known, but have not been named owing to lack of material.

Malaria parasites (*Plasmodium*) are relatively uncommon. They have been recorded in sparrows, a starling, a falcon, a seagull, and four species of wild anseriform birds.

Haemoproteus is common. Seven named species have been recorded, but many birds are known to harbour parasites of this genus, some of which may be new.

Leucocytozoon is fairly common. Five species have been recorded, and several other unnamed parasites are known to occur.

Lankesterella picumni, sp.nov., is described from *Climacteris picumnus*, being apparently the first record of a haemogregarine from a bird in Australia.

Lankesterella paddae is known in sparrows, and possibly silvereyes.

I. INTRODUCTION

The value of studying avian blood parasites can hardly be overemphasized. Many important discoveries have been made as a result of research on parasites of birds, for example, recognition of the sexual nature of exflagellation (MacCallum 1898), development of the sexual stages in mosquitoes (Ross 1898, 1899), recognition of exo-erythrocytic schizogony in malaria parasites (Raffaele 1936; James and Tate 1937), and definition of the pre-erythrocytic cycle (Reichenow and Mudrow

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1943; Huff and Coulston 1944). The value of small birds for laboratory studies of chemotherapy was recognized after World War I, and the plasmodicidal effects of plasmoquine and atebrin were demonstrated on avian malaria in Germany. During World War II, very large numbers of newly hatched chickens, ducklings, etc., were used in screening possible antimalarial compounds. It was in this way that the plasmodicidal action of paludrine was discovered.

In other parts of the world, serious outbreaks of disease in domestic birds are caused by parasites derived from wild birds. For example, ducks in North America may develop splenomegaly and a severe anaemia, which may be fatal, due to infection with a *Leucocytozoon*. In Africa, a *Plasmodium* of wild birds is highly pathogenic to domestic turkeys. Fortunately, no epizootics of this kind have been reported in Australia.

The present paper is a sequel to an earlier review of the blood parasites of Australian mammals (Mackerras 1959), and the general arrangement is the same. The available material is much scantier, but it still seems desirable to bring together all that is known for the benefit of future workers, even though we lack the temerity (or the type material) to attach specific names to many of the parasites recorded. Publications also are fewer. Indeed, except for the studies of Lawrence (1946) on the malaria parasites of sparrows and starlings in Sydney, very little has been published on the protozoan blood parasites of Australian birds since the pioneering work of J. B. Cleland, T. H. Johnston, J. A. Gilruth, and A. Breinl in the early part of this century.

The spirochaetal genus *Borrelia*, which was included among the haematozoa of mammals, has been omitted from this paper, because only one avian species is known in Australia. This is the introduced *B. anserina* (Sakharoff), which infects domestic fowls, and is transmitted by the fowl-tick, *Argas persicus* (Oken), and the mite, *Dermanyssus gallinae* (Redi). It was recorded by Johnston (1910), and has been reviewed by Seddon (1953).

II. Methods

Thin blood films were dried in the air and stained with Leishmann's stain, or fixed in pure methanol and stained with dilute Giemsa's stain. Organ smears and sections were also examined when available.

When describing trypanosomes, we have followed the nomenclature of Wenyon (1926), and have used the following abbreviations:

L	Length of body, measured along the mid-line.
B	Maximum breadth, including the undulating membrane.
PK	Distance from posterior end to the kinetoplast.
KN	Distance from the kinetoplast to the posterior edge of the nucleus.
NA	Distance from the anterior edge of the nucleus to the anterior end of the body.
FF	Length of the free flagellum.

The classification of the parasites follows Kudo (1954), with additions, and that of the birds has been taken from "An Australian Bird Book" by J. A. Leach, 9th Ed., 1958, revised by P. Crosbie Morrison. The synonymy has been taken from the R.A.O.U. "Official Checklist of the Birds of Australia", 2nd Ed., 1926.

III. Host–Parasite List

Classification and Name of Host	Parasite
GALLIFORMES	
Megapodiidae	
Alectura lathami Gray, 1831, scrub turkey	*Haemoproteus* sp.
Phasianidae	
Gallus domesticus Linnaeus, 1758, domestic fowl	*Borrelia anserina* Sakharoff
COLUMBIFORMES	
Columbidae	
Ptilinopus superbus (Temminck, 1811), purple-crowned pigeon	*Haemoproteus columbae* Kruse
Columba livia Gmelin, 1789, domestic pigeon	*Haemoproteus columbae* Kruse
CHARADRIIFORMES	
Laridae	
Larus novae-hollandiae Stephens, 1826, silver gull	*Plasmodium* sp.
Otididae	
Eupodotis australis (Gray, 1829), plain turkey	*Haemoproteus* sp.
CICONIIFORMES	
Ardeidae	
Notophoyx novae-hollandiae (Latham, 1790), white-faced heron	*Trypanosoma notophoyxis* Breinl *Haemoproteus* sp.
Demigretta sacra (Gmelin, 1789), reef heron	*Trypanosoma ?notophoyxis* Breinl
ANSERIFORMES	
Anatidae	
Cygnus atratus (Latham, 1790), black swan	*Plasmodium biziurae* (Gilruth, Sweet, & Dodd)
Casarca tadornoides (Jardine & Selby, 1828), chestnut-breasted shelduck	*Haemoproteus nettionis* (Johnston & Cleland)
Anas superciliosa Gmelin, 1789, black duck	*Plasmodium biziurae* (Gilruth, Sweet, & Dodd) *Haemoproteus nettionis* (Johnston & Cleland)
Anas castanea (Eyton, 1838), chestnut teal	*Haemoproteus nettionis* (Johnston & Cleland)
Malacorhynchus membranaceus (Latham, 1801), pink-eared duck	*Plasmodium biziurae* (Gilruth, Sweet, & Dodd)
Biziura lobata (Shaw, 1796), musk duck	*Plasmodium biziurae* (Gilruth, Sweet, & Dodd)
PELECANIFORMES	
Phalacrocoracidae	
Phalacrocorax melanoleucus (Vieillot, 1817), little pied cormorant	*Leucocytozoon vandenbrandeni* Rodhain

Classification and Name of Host	Parasite
FALCONIFORMES	
Accipitridae	
Haliastur indus (Boddaert, 1783), white-headed sea-eagle	*Trypanosoma* sp. *Haemoproteus* sp.
Falconidae	
Falco hypoleucus Gould, 1840, grey falcon	*Trypanosoma* sp. *Plasmodium* sp.
STRIGIFORMES	
Strigidae	
Ninox novae-seelandiae (Gmelin, 1788), boobook owl	*Trypanosoma* sp. *Haemoproteus noctuae* Celli & San Felice *Leucocytozoon danilewskyi* Ziemann
Ninox strenua (Gould, 1838), powerful owl	*Haemoproteus noctuae* Celli & San Felice
PSITTACIFORMES	
Psittacidae	
Platycercus adelaidae Gould, 1840, Adelaide rosella	*Haemoproteus* sp.
Barnardius semitorquatus (Quoy & Gaimard, 1830), twenty-eight parrot	*Haemoproteus* or *Plasmodium* sp.
Kakatoë galerita (Latham, 1790), white cockatoo	*Haemoproteus* sp.
CAPRIMULGIFORMES	
Podargidae	
Podargus strigoides (Latham, 1801), tawny frogmouth	*Haemoproteus* sp. *Leucocytozoon caprimulgi* Kerandel
CORACIIFORMES	
Alcedinidae	
Dacelo gigas (Boddaert, 1783), kookaburra	*Haemoproteus* sp.
Meropidae	
Merops ornatus Latham, 1801, bee-eater	*Haemoproteus* sp.
CUCULIFORMES	
Cuculidae	
Eudynamys orientalis (Linnaeus, 1766), koel	*Haemoproteus* sp.
PASSERIFORMES	
Muscicapidae	
Microeca fascinans (Latham, 1801), jacky winter	*Trypanosoma* sp. *Haemoproteus* sp.
Petroica phoenicea Gould, 1837, flame robin	*Haemoproteus* sp.
Myiagra rubecula (Latham, 1801), leaden flycatcher	*Haemoproteus* sp.
Timaliidae	
Pomatostomus superciliosus (Vigors & Horsfield, 1827), white-browed babbler	*Haemoproteus* sp.

Classification and Name of Host	Parasite
Sylviidae	
Gerygone olivacea (Gould, 1838), white-throated warbler	*Haemoproteus* sp.
Megalurus gramineus (Gould, 1845), little grassbird	*Haemoproteus* sp.
Grallinidae	
Grallina cyanoleuca (Latham, 1801), peewee	*Haemoproteus* sp.
Pachycephalidae	
Pachycephala ?melanura Gould, 1842, black-tailed whistler	*Trypanosoma* sp.
Turdidae	
Oreocincla lunulata (Latham, 1801), ground-thrush	*Haemoproteus geocichlae* (Cleland & Johnston)
Cracticidae	
Gymnorhina tibicen (Latham, 1801), black-backed magpie	*Trypanosoma* sp. *Haemoproteus* sp. *Leucocytozoon* sp.
Gymnorhina hypoleuca (Gould, 1837), white-backed magpie	*Haemoproteus* sp.
Cracticus torquatus (Latham, 1801), grey butcher-bird	*Haemoproteus* sp.
Strepera graculina (Shaw, 1790), pied currawong	*Haemoproteus* sp. *Leucocytozoon* sp.
Paridae	
Aphelocephala leucopsis (Gould, 1841), eastern whiteface	*Haemoproteus* sp.
Certhiidae	
Climacteris picumnus Temminck, 1824, brown tree-creeper	*Leucocytozoon* sp. *Lankesterella picumni*, sp.nov.
Zosteropidae	
Zosterops lateralis (Latham, 1801), grey-breasted silvereye	*Haemoproteus* sp. *Lankesterella paddae* (Aragão)
Dicaeidae	
Dicaeum hirundinaceum (Shaw, 1792), mistletoe bird	*Haemoproteus* sp.
Pardalotus melanocephalus (Gould, 1838), chip-chip	*Trypanosoma* sp. *Haemoproteus* sp. *Leucocytozoon* sp.
Meliphagidae	
Melithreptus lunatus (Vieillot, 1802), white-naped honeyeater	*Haemoproteus* sp.
Melithreptus validirostris (Gould, 1837), strong-billed honeyeater	*Haemoproteus* sp.
Melithreptus brevirostris (Vigors & Horsfield, 1827), brown-headed honeyeater	*Haemoproteus* sp.

Classification and Name of Host	Parasite
Myzomela sanguinolenta (Latham, 1801), blood bird	*Trypanosoma* sp. *Haemoproteus* sp. *Leucocytozoon anellobiae* Johnston
Meliphaga fusca Gould, 1837, brown honeyeater	*Trypanosoma* sp. *Haemoproteus ptilotis* (Cleland & Johnston) *Leucocytozoon anellobiae* Johnston
Meliphaga virescens (Vieillot, 1817), singing honeyeater	*Haemoproteus ptilotis* (Cleland & Johnston)
Meliphaga chrysops (Latham, 1801), yellow-faced honeyeater	*Trypanosoma* sp. *Haemoproteus ptilotis* (Cleland & Johnston)
Meliphaga melanops (Latham, 1801), yellow-tufted honeyeater	*Haemoproteus ptilotis* (Cleland & Johnston)
Meliphaga plumula (Gould, 1841, yellow-fronted honeyeater	*Haemoproteus ptilotis* (Cleland & Johnston)
Meliphaga penicillata Gould, 1837, white-plumed honeyeater	*Haemoproteus ptilotis* (Cleland & Johnston)
Meliornis novae-hollandiae (Latham, 1790), yellow-winged honeyeater	*Haemoproteus meliornis* (Cleland & Johnston)
Myzantha melanocephala (Latham, 1801), soldier bird	*Trypanosoma myzanthae*, sp.nov. *Haemoproteus* sp. *Leucocytozoon anellobiae* Johnston
Myzantha flavigula Gould, 1840, yellow-throated miner	*Haemoproteus* sp.
Anthochaera chrysoptera (Latham, 1801), little wattle-bird	*Trypanosoma anellobiae* Cleland & Johnston *Haemoproteus* sp. *Leucocytozoon anellobiae* Johnston
Acanthagenys rufogularis Gould, 1838, spiny-cheeked honeyeater	*Haemoproteus* sp. *Leucocytozoon anellobiae* Johnston
Entomyzon cyanotis (Latham, 1801), blue-faced honeyeater	*Trypanosoma* sp. *Haemoproteus* sp. *Leucocytozoon anellobiae* Johnston
Philemon corniculatus (Latham, 1790), leatherhead	*Haemoproteus philemon* (Cleland & Johnston) *Leucocytozoon anellobiae* Johnston
Fringillidae	
Passer domesticus (Linnaeus, 1758), common sparrow	*Plasmodium relictum* (Grassi & Feletti) *Lankesterella paddae* (Aragão)
Sturnidae	
Sturnus vulgaris (Linnaeus, 1758), starling	*Plasmodium relictum* (Grassi & Feletti)
Oriolidae	
Oriolus sagittatus (Latham, 1801), olive-backed oriole	*Trypanosoma* sp. *Haemoproteus* sp. *Leucocytozoon* sp.
Sphecotheres vieilloti Vigors & Horsfield, 1827, southern figbird	*Leucocytozoon* sp.
Dicruridae	
Chibia bracteata (Gould, 1842), spangled drongo	*Haemoproteus* sp.

Classification and Name of Host	Parasite
Ptilonorhynchidae	
Ptilonorhynchus violaceus (Vieillot, 1816), satin bower-bird	*Haemoproteus* sp. *Leucocytozoon* sp.
Ailuroedus crassirostris (Paykull, 1815), green catbird	*Leucocytozoon* sp.
Chlamydera nuchalis (Jardine & Selby, 1830), great bower-bird	*Trypanosoma chlamydoderae* Breinl *Haemoproteus* sp.
Corvidae	
Corcorax melanorhamphus (Vieillot, 1817), white-winged chough	*Leucocytozoon sakharoffi* Sambon

Scott (1927) found parasites, which were either *Plasmodium* or *Haemoproteus*, in a *Barnardius semitorquatus* from Australia, and recorded a triple infection with *Plasmodium*, *Haemoproteus*, and *Leucocytozoon* in a wompoo pigeon, *Megaloprepia magnifica* (Temminck), probably from Australia or New Guinea. Both birds died in the London Zoological Gardens.

Fonseca (1938) described *Trypanosoma fulicae* and *Haemoproteus fulicae* from the coot, *Fulica atra* L., 1758, in India. This bird occurs also in Australia, and one specimen from Myall Lakes, N.S.W., has been examined, but no parasites were seen.

IV. Class MASTIGOPHORA

Genus TRYPANOSOMA Gruby

TRYPANOSOMA NOTOPHOYXIS Breinl

Trypanosoma notophoyxis Breinl, 1913, p. 33.

Hosts.—Notophoyx novae-hollandiae (Latham), ?*Demigretta sacra* (Gmelin).

Distribution.—Townsville, ?Mornington I., N. Qld.

Breinl found trypanosomes in 1 out of 6 birds examined. Two types of parasites were observed: long, slender forms and broad, spindle-shaped forms. The former (Plate 1, Fig. 7) were from 27 to 32 μ long, excluding the free flagellum. The kinetoplast was large, and the nucleus well-stained, usually extending across the whole width of the parasite, and often placed obliquely. Cytoplasm was dark blue, without striations or granules.

Parasites of the second type (Plate 1, Fig. 6) were 32–36 μ long, and pointed at both ends. The nucleus was large, reddish, and surrounded by a lighter zone. Cytoplasm was dark blue, with vacuoles ("probably artifacts") and longitudinal striations. The undulating membrane was well developed, and the flagellum shorter and slightly thinner than in the slender forms.

What is possibly the same species was found in small numbers in the blood of a *Demigretta sacra* at Mornington I., Gulf of Carpentaria, in May 1951. They were moderate-sized, plump trypanosomes, with the undulating membrane usually wound around the body, and a rather fine, free flagellum (Plate 2, Figs. 1–3). The anterior extremity usually ended in a short, beak-like process. Some very broad forms, with a band-like, transversely placed nucleus, were observed. The kinetoplast was large, round, and situated close to the posterior end. They were distinctly smaller than Breinl's specimens, as a comparison of dimensions (in μ) shows:

	T. notophoyxis (first type)	*T. notophoyxis* (second type)	Specimens from *D. sacra*
L	27–32	32–36	21–26
B	3–4	7–8	6–10
PK	3		1·5–3
KN	12–14	14	7–11
NA			6–11
FF	8	4–5	9–11

TRYPANOSOMA sp.

Breinl (1913) described small and large forms in *Falco hypoleucus* Gould, and large forms in *Haliastur indus* (Boddaert) (syn. *girrenera*), from Townsville, all of which he allocated to *T. avium.*

The small forms in the falcon (Plate 1, Fig. 2) were described as resembling somewhat the forms seen in a chronic infection with *T. lewisi*. Both ends were pointed, and the nucleus extended across the width of the body. The cytoplasm stained light blue with Giemsa's stain, and showed no striations, but contained scattered reddish granules. The undulating membrane was distinct, but not pronounced.

The large forms (Plate 1, Fig. 3) tapered to both ends. A vacuole was sometimes seen in front of the kinetoplast. The nucleus stained well, and filled the entire width of the parasite. The cytoplasm was filled with reddish granules, and was without striation. The undulating membrane was distinct, and the flagellum fairly fine.

The parasites from the eagle (Plate 1, Fig. 1) were very similar, but the cytoplasm stained dark blue, and showed distinct striation. The undulating membrane was broad. The dimensions (μ) were given as follows:

	Falcon		Eagle
	Small Forms	Large Forms	
L	35–40	44·5–58·5	44·5–58·5
B	3·5	6–7	7–9
PK	10	10–15	6–11
KN	7–10	12–15	12–16·5
FF	5–7	6–7	4–6

It seems almost certain that the large forms from both hosts belong to the same species, and the presence of smaller forms in the falcon may only indicate that multiplication of the parasite was occurring.

The name *T. mesnili* was used by Novy and MacNeal (1905) for a parasite of a North American hawk. Their figure depicts a rather large, broad trypanosome not particularly like Breinl's figures. His slides are so faded that they cannot be used, and more material is needed to decide the status of the Australian parasites.

TRYPANOSOMA sp.

Breinl (1913) gave a brief description of a small trypanosome seen in the blood of 1 out of 4 *Ninox novae-seelandiae* (Gmelin) (syn. *boobook*). The infection was very scanty, only two trypanosomes being found, one in a wet preparation, and one in 20 stained films. He described it as short and stumpy, with dark, bluish-staining, distinctly striated cytoplasm, large nucleus, and short, free flagellum (Plate 1, Fig. 8). The dimensions were: L, 26 μ; B, 3 μ; PK, 3 μ; KN, 9 μ.

He did not propose a name for this species. It may be close to *Trypanosoma noctuae* Schaudinn of the little European owl, *Athene noctua*, but more material is needed to decide whether it is the same.

THE STATUS OF TRYPANOSOMA AVIUM DANILEWSKY, 1885

On morphological grounds, many observers concluded that one species of trypanosome, *T. avium*, was present in many unrelated birds. Danilewsky originally described *T. avium* from two hosts, an owl of undetermined species and a roller, so that it is possible that he had two species of trypanosomes before him at the time. Laveran (1903) described and figured a species, which he regarded as *T. avium*, from an owl, *Syrnium aluco*. This organism was fusiform; the length, including the flagellum, was 33–45 μ; the nucleus lay about the middle of the body; and the large, spherical kinetoplast lay some distance from the sharply pointed, posterior end. The figures depict a long slender trypanosome, with well-developed undulating membrane showing a few large undulations, and a well-defined free flagellum.

It seems reasonable to restrict the use of the name *T. avium* Danilewsky, Laveran emend. to those parasites of owls which conform to the description given by Laveran, and to use other names for parasites from other hosts, even though they may appear very similar. This would seem to cause less confuson, than lumping together forms which may or may not be conspecific. No trypansomes corresponding to *T. avium* have yet been seen in Australian owls.*

TRYPANOSOMA ANELLOBIAE Cleland & Johnston

Trypanosoma anellobiae Cleland and Johnston, 1910, p. 105.

Host.—*Anthochaera chrysoptera* (Latham), previously known as *Anellobia chrysoptera*, hence the specific name of the parasite.

Distribution.—Brisbane, Eidsvold, Qld.

Cleland and Johnston originally studied very scanty infections in blood films of 2 out of 11 *A. chrysoptera* obtained near Brisbane by Dr. T. L. Bancroft. The trypanosomes were about 35 μ in length, and very narrow. The middle portion was uniform in breadth, but gradually narrowed anteriorly and posteriorly to pointed ends. The anterior extremity was longer and narrower than the posterior. The kinetoplast was 3 μ from the posterior end. The part between this and the end was only slightly stained, whereas the rest of the body was deeply coloured by Giemsa. The undulating membrane was extremely narrow. Nucleus and flagellum were not stained.

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* Since this was written, our attention has been drawn to a series of papers by Baker (1956) on the life history of the trypanosome found in rooks and jackdaws in England. He found that it was transmitted by the louse fly, *Ornithomyia avicularia* L., and infected canaries and a missel thrush experimentally. He identified the organism as *T. avium* Danilewsky, although infectivity to owls was not studied.

In a subsequent publication (Cleland and Johnston 1911), they enlarged on their previous account, after studying another series of films sent by Dr. Bancroft from Eidsvold. Three figures of trypanosomes from *A. chrysoptera* depict a rather slender trypanosome, with a narrow undulating membrane, and a very short, free flagellum. The nucleus lay in the posterior half of the body, and was small, rounded, or elongate in the long axis (Figs. 1–3). The authors, however, remarked on the great variation in width observed, some parasites being "very broad and others extremely narrow".

TRYPANOSOMA MYZANTHAE, sp. nov.

Host.—*Myzantha melanocephala* (Latham).

Distribution.—Eidsvold, Qld.

Type.—Slide in the collection of the Queensland Museum, Brisbane.

Parasites were found in 3 out of 4 soldier birds examined; the infections were very scanty in two, and moderately numerous in the third.

Morphology (Plate 2, Figs. 4–6)

A moderate-sized, rather robust-looking trypanosome; with pointed posterior end; nucleus near the mid-point of the body, often band-like; well-developed undulating membrane, usually wound once around the body; and a relatively stout, free flagellum. The kinetoplast was large, oval, and situated close to the posterior end. Myonemes were not detected. The trypanosomes were fairly uniform in size, and no dividing forms were seen.

Dimensions.—L, 19–24 μ; B, 6·5–7 μ; PK, 1·5 μ or less; KN, 7–7·5 μ; NA, 7–10 μ; FF, 4–9 μ.

T. myzanthae differs from *T. anellobiae* in shape, being usually broader, in the position of the undulating membrane, usually wound around the body, in the central position of the nucleus, and in the longer, thicker, free flagellum. It is like the specimens of *T. notophoyxis* from *Demigretta sacra*, but differs from them in dimensions and oval kinetoplast.

TRYPANOSOMA sp.

A puzzling diversity of forms was found in a specimen of *Meliphaga chrysops* (Latham) from Myall Lakes, N.S.W., and Cleland and Johnston (1911) found a rather similar condition in two other birds. *Meliphaga fusca* Gould and *Entomyzon cyanotis* (Latham).

A moderate infection was found in the only specimen of *M. chrysops* examined. The commonest form was a short, broad trypanosome. The kinetoplast was close to the posterior end, and the nucleus was often band-like, about 7 by 2·5 μ, and transversely placed near the mid-point of the body. The posterior end was usually rounded (Plate 2, Figs. 7 and 8). The undulating membrane was usually wound around the body, and the free flagellum very short.

Two much larger forms were also seen. One of these was long and slender, lying in the C-position, with the undulating membrane along the convex border, and the nucleus in the posterior half of the body. The kinetoplast was an elongated rod with knobbed ends, and the free flagellum was difficult to make out, but appeared to be very short (Plate 2, Fig. 9). This single specimen resembled the figures of *T. anellobiae*. The other large specimen was much stouter, with a rounded posterior end, the oval nucleus situated in the posterior half of the body close to the convex border, and a short, free flagellum. Distinct myonemes were present (Plate 2, Fig. 10). Dimensions (μ) are as follows:

	Squat Forms	Long Forms	
L	11·5–17	26	31
B	7–8	5	6·5
PK	0·5–2	0	2·5
KN	5·5–7	5	9·5
NA	1·5–8	15	17
FF	6–10	*c.*8	*c.*5

We consider that these trypanosomes are probably the same species as those from *M. fusca* allotted to *T. anellobiae* by Cleland and Johnston (1911). Their material consisted of trypanosomes found in 4 out of 11 specimens of *Meliphaga fusca* Gould (syn. *Ptilotis fusca*), from Eidsvold. They were described as varying from moderately narrow, through a fusiform shape, to broad forms. The nucleus was a little in front of the centre. The kinetoplast was close to the posterior end in some, but decidedly further forward in others. The undulating membrane wound round the body, ending in a moderately short flagellum (Figs. 10–12). The same authors found trypanosomes in 3 out of 7 specimens of *Entomyzon cyanotis* (Latham) from the same locality, also recording them as *T. anellobiae*. They remarked, however, on the great diversity of forms seen. In one bird the parasites were very narrow, in another fairly broad, while the third infected bird had a mixture of both types (Figs. 8 and 9).

It is difficult to place these diverse forms without new material and experiment. They do not seem clearly to belong either to *T. anellobiae* or *T. myzanthae*, but possibly there is only one, extremely variable species in honeyeaters.

Cleland (1922) recorded trypanosomes in *E. cyanotis* from Bumberry, in *Meliphaga chrysops* from Milson I. in the Hawkesbury R., and in *M. fusca* from Grafton, all in New South Wales.

TRYPANOSOMA sp.

A trypanosome in the blood of 1 out of 5 *Myzomela sanguinolenta* (Latham) obtained at Eidsvold was described by Cleland (1915) as follows: "The posterior end of the only uninjured trypanosome seen was finely attenuate with the micronucleus

12 μ* from the extremity. The macronucleus, 2·5 μ long, was 11 μ anteriorly, the body at this level being 5 μ wide. From the macronucleus the parasite gradually tapered anteriorly to end at 26 μ. There was a broad, undulating membrane." This species seems to differ from *T. anellobiae* and *T. myzanthae*, both of which have a narrow undulating membrane.

TRYPANOSOMA CHLAMYDODERAE Breinl

Trypanosoma chlamydoderae Breinl, 1913, p. 32.

Host.—*Chlamydera nuchalis* (Jardine & Selby), previously identified as *Chlamydodera orientalis* Gould, hence the specific name of the parasite.

Distribution.—Townsville, Qld.

Breinl found scanty trypanosomes in 1 out of 5 bower-birds examined. Two distinct forms were observed, a slender form of stiff appearance, possessing darkly staining cytoplasm, and a broader form staining lightly. No striations were visible in either form. The broad forms were of a distinctive appearance, with broad middle section tapering to both ends. The undulating membrane was not well developed, and the flagellum was very slender. The dimensions (in μ) were:

	Slender Forms	Broad Forms
L	34–38	35–40
B	2–3	6–8
PK	4·5	3
KN	10–13	12
FF	3	3

Breinl regarded the smallness of the nucleus and kinetoplast as distinctive (Plate 1, Figs. 4–5).

TRYPANOSOMES OF OTHER PASSERINE BIRDS

(1) Trypanosomes were found in 1 out of 10 *Microeca fascinans* (Latham), obtained at Eidsvold. Cleland and Johnston (1911) stated that the posterior end was broad, the body then narrowing rapidly to end in a short beak. Cytoplasm was deep blue, sometimes alveolar, or showing streaky lines of fine bluish granules. The nucleus was central and the kinetoplast a large, conspicuous, deep purple dot or rod near the posterior end. A narrow undulating membrane was visible, but the flagellum was not definitely recognizable.

(2) Trypanosomes were recorded in *Pachycephala melanura* Gould, from Stradbroke I., Qld., by Cleland (1922), but were not described or named. This should probably be recorded under another species of whistler, as *melanura* is a Western Australian bird.

(3) A single trypanosome was found by the authors in a *Gymnorhina tibicen* (Latham) collected near Brisbane. It was a small, relatively broad organism, with the following measurements: L, 17 μ; B, 7 μ; PK, 2 μ; KN, 6 μ; NA, 6·5 μ; FF, 10 μ.

(4) Cleland and Johnston (1911) recorded trypanosomes in 1 out of 14 specimens of *Pardalotus melanocephalus* Gould, obtained at Eidsvold. They described

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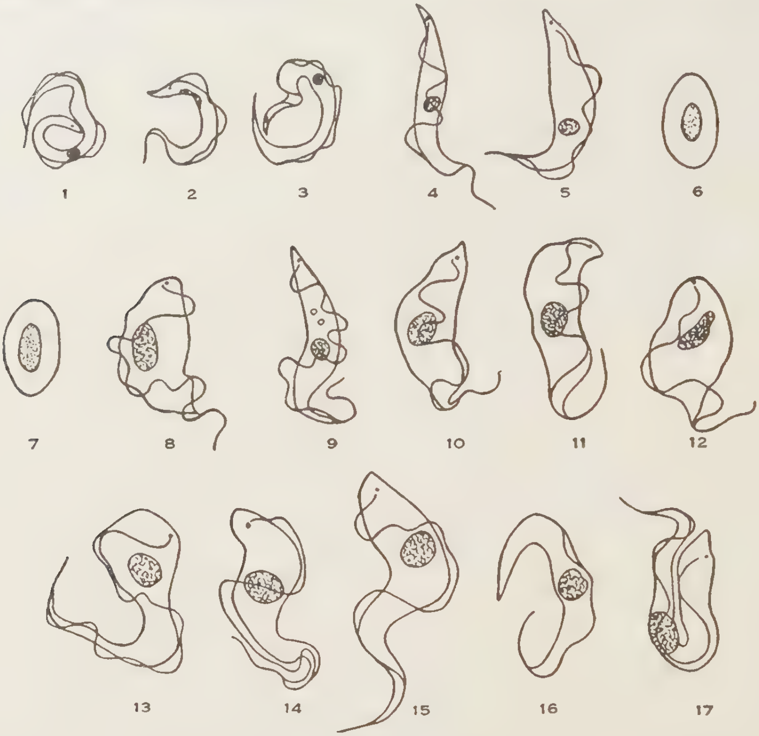
* This is possibly a misprint for 1–2 μ.

them as large and conspicuous, with a broad, blunt posterior end, from which the body narrowed uniformly to end in an elongate anterior end. The cytoplasm was deep blue, with an alveolar appearance. The nucleus was large and central, and the kinetoplast a deep purple spot close to the posterior end. The undulating membrane wound around the body, ending in a short, free flagellum.

They did not give measurements, but their figures (cf. Figs. 13–17) depict an organism twice to three times as broad as *T. anellobiae*, with a large, rounded nucleus. In three trypanosomes the nucleus was placed well posterior to the mid-point, in one it was central, and in one anterior to the mid-point. This appears to be distinct from the parasites of the honeyeaters, differing from *T. anellobiae* in body size, particularly in breadth, and in the broadness of the posterior end, and from *T. myzanthae* in length, in the shape of the body and nucleus, shortness of flagellum, and conformation of the undulating membrane, having relatively few, large convolutions in contrast to more numerous, smaller ones.



Figs. 1–17.—Trypanosomes of Australian birds; rearranged from Cleland and Johnston (1911), Plates XXX and XXXI. 1–3, *T. anellobiae* in *Anthochaera chrysoptera*; 4–6, trypanosomes and red cell in *Oriolus sagittatus*; 7–9, red cell and trypanosomes in *Entomyzon cyanotis*; 10–12, trypanosomes in *Meliphaga fusca*; 13–17, trypanosomes in *Pardalotus melanocephalus*.

(5) Cleland and Johnston (1911) found trypanosomes in 1 out of 5 orioles, *Oriolus sagittatus* Latham, taken at Eidsvold. They stained deep blue, were very narrow, and had a central nucleus and a marked kinetoplast near the posterior

end. The undulating membrane was narrow, and the free flagellum short (Figs. 4 and 5).

This trypanosome may be *T. chlamydoderae*, the figures agreeing fairly well with those of Breinl. It resembles that species in having a small, round nucleus, and a sharply pointed posterior end. The nucleus, however, was placed centrally, whereas in *chlamydoderae* it was well posterior to the mid-point.

V. Class SPOROZOA

Order HAEMOSPORIDIA

Genus PLASMODIUM Marchiafava & Celli

Several species of avian malaria parasites have been studied by many workers in other parts of the world, and the details of their life histories are now well known. All so far investigated have been transmitted by mosquitoes, and the sequence of events in the insect has followed the same pattern. Fertilization and ookinete formation occur in the midgut of the mosquito, the oocyst develops on its coelomic surface, the sporozoites are liberated into the haemocoele when the oocyst bursts, and they then make their way to the salivary glands. When the sporozoites are injected into the skin of a susceptible bird, small, pre-erythrocytic schizonts develop in macrophages at the site of inoculation. Merozoites liberated by these schizonts initiate the erythrocytic cycle. Another series of exo-erythrocytic schizonts, which may be very large, develops in the endothelial cells of various organs. These may be found after blood inoculation, as well as in sporozoite-induced infections.

Trophozoites of various ages, schizonts, and gametocytes occur in red cells. The presence of schizonts in the peripheral blood distinguishes *Plasmodium* from *Haemoproteus*. However, the discovery of species of *Plasmodium* which produce elongate, halter-shaped gametocytes throws considerable doubt upon identifications of *Haemoproteus* based on single dried films.

If dried blood films alone are available, only the morphology of the erythrocytic parasites, their effect on the host cell, and the types of cells infected can be recorded. If a series of films is available, it may be possible to determine the length of the asexual cycle. If an infected bird is available, subinoculation to a susceptible host may allow studies on host-specificity, pathogenicity, intermediate hosts, and reaction to drugs. The canary has proved a useful bird for subinoculation experiments, being susceptible to the species found in sparrows and in some other passerine birds, e.g. the cliff swallow. It is, however, refractory to the parasites of fowls and pheasants. Chickens can be used for these, and ducklings and young turkeys have also proved susceptible to some species.

PLASMODIUM BIZIURAE (Gilruth, Sweet, & Dodd)

Proteosoma biziurae Gilruth, Sweet, and Dodd, 1910, p. 231.
Plasmodium biziurae (Gilruth, Sweet, and Dodd), Coatney and Roudabush, 1949, p. 2.

Hosts.—Biziura lobata (Shaw), *Cygnus atratus* (Latham), *Anas superciliosa* (Gmelin), *Malacorhynchus membranaceus* (Latham).

Distribution.—?Victoria; Glen Davis, N.S.W.; Eidsvold, Qld. Gilruth, Sweet, and Dodd described the parasite from two musk ducks which died in the Zoological Gardens, Melbourne. The localities from which the birds had come were not recorded. The musk duck has a wide range, from Rockhampton in Queensland, round the southern part of Australia, to North West Cape in Western Australia.

Morphology (Plate 3, Figs. 1–3)

Both the original infections were scanty, and only young forms and mature gametocytes were seen. The young parasites were elongate, and contained fine pigment granules. Mature gametocytes varied from 8·5 to 10 μ in length by 4·8 to 9·7 μ in width. The female gametocytes were usually spherical, with a clearly defined nucleus, and a more or less general distribution of large pigment granules. The male gametocytes were usually oval, with hyaline cytoplasm, diffuse nucleus, and a polar distribution of the pigment. The infected cells were enlarged and distorted, their nuclei usually lying obliquely across one end of the cell.

Cleland (1915) studied the parasites in a film from a black swan, sent to him from Eidsvold by Dr. T. L. Bancroft. He found large, rounded, or irregularly oval gametocytes. Some were bean-shaped, and a few tended to curl round the host nucleus after the fashion of a *Haemoproteus*. They usually displaced the nuclei of the infected cells, some of which were partly de-haemoglobinized. He could not find any schizonts, but thought the parasite was probably a *Plasmodium* on account of the absence of well-marked halteridium forms.

We have seen similar parasites in films from *Anas superciliosa* and *Malacorhynchus membranaceus* lent by Mr. A. J. Bearup, and in films from *A. superciliosa* sent to us by the Reverend R. Palmer, who also preserved pieces of liver, spleen, heart, and lung. Parasites were rather scanty in a film from heart blood, only young rings, amoeboids, and gametocytes being found. They were even more difficult to find in a smear made from liver, and no schizogonic stages were seen. Sections of the organs were searched unsuccessfully for exo-erythrocytic forms.

The parasites conformed closely to the description given by Gilruth, Sweet, and Dodd. The youngest stages seen were minute rings (Plate 3, Fig. 1) about 1·5 μ in diameter. Slightly larger, solid, amoeboid forms, with central nucleus and fine pigment granules, were also present. The female gametocytes (Plate 3, Fig. 3) were usually spherical or oval, from 6 to 10 μ in length by 5 to 6·5 μ in width; the nucleus was central, or slightly nearer one side, and was surrounded by a clear halo; pigment was dark brownish black, often varying in the one cell from fine points to irregular, coarse granules scattered throughout the cytoplasm. Male gametocytes (Plate 3, Fig. 2) were from 9 to 11 μ long by 4·5 to 5 μ wide, usually paler than the female, and with less well-defined nucleus; the pigment was sometimes scattered, sometimes in two groups, one at each end of the parasite. The red cells were slightly enlarged, and their nuclei usually displaced. No halteridium forms were seen.

This is evidently not a very common parasite in ducks, as none was found in an examination of 76 films from black ducks from Townsville and Brisbane. It probably belongs to the *relictum* group of bird *Plasmodium*, that is, to those species that are characterized by round or irregular gametocytes, displacing the host cell nucleus. It differs from *P. relictum* in introduced sparrows by its large size and coarser, more abundant pigment.

PLASMODIUM RELICTUM (Grassi & Feletti)

Haemamoeba relicta Grassi and Feletti, 1891, p. 19.

Plasmodium passeris Johnston and Cleland, 1909, p. 505.

Australian hosts.—Passer domesticus (L.), *Sturnus vulgaris* L.

Australian distribution.—Sydney; Brisbane.

In 1890, Grassi and Feletti described an amoeboid blood parasite of sparrows in Italy as *Haemamoeba praecox*, but in a note to the paper they stated that the same species caused quotidian fever in man. A year later, they described as *Haemamoeba relicta* another parasite of sparrows, which they thought was distinct from *praecox*. Gradually, the specific name *praecox* came into use for the parasite of malignant tertian malaria of man, now known as *P. falciparum*, although in the early part of this century other workers were recording all bird malarias as *praecox*. To avoid further confusion, the specific name *praecox*, though valid, has been dropped altogether by recent workers, and *P. relictum* has been accepted as if it were the first malaria parasite of sparrows to be described.

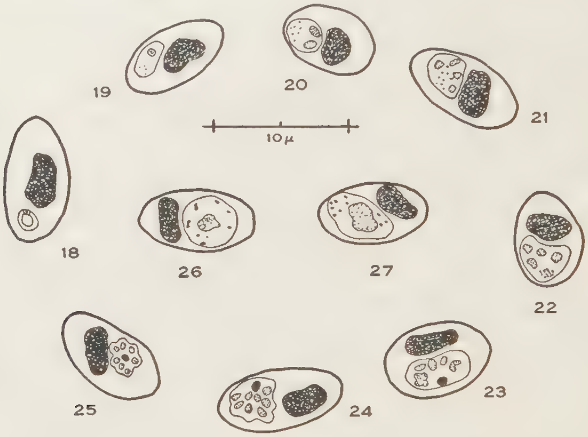
No less than nine species of *Plasmodium* have been described in sparrows in various parts of the world, of which four are regarded as valid (Hewitt 1949). They are *P. relictum*, *P. cathemerium* Hartman, which is separated from *relictum* by the shape of the granules of pigment, *P. elongatum* Huff, which has peculiarly elongated merozoites and gametocytes, and *P. rouxi* Sergent, Sergent, & Catanei, which produces only four merozoites.

P. relictum has been found in Australia in two species of introduced birds, *Passer domesticus* (L.), the house sparrow, and *Sturnus vulgaris* L., the starling. Johnston (1909) recorded it from sparrows in Sydney, at first as "closely resembling *Plasmodium praecox*", but, as the description of *praecox* available at that time referred to the human parasite, he concluded that the parasites of the sparrow were distinct, and in the same year he and Cleland described it as a new species, *Plasmodium passeris*.

Lawrence (1946) found 65 out of 91 sparrows examined in Sydney to be infected with malaria parasites. He was unable to separate *P. relictum* and *P. cathemerium* in these sparrows, because the clear-cut differences in the shape of the granules of pigment described by workers in other parts of the world did not occur. Lawrence also recorded *P. relictum* in 1 out of 2 starlings examined, and transmitted the infection to sparrows by blood inoculation.

Morphology (Figs. 18–27)

We have seen moderately numerous infections in two sparrows from Sydney, one of which was picked up in an almost moribund condition, and scanty infections in 8 out of 78 sparrows examined in Brisbane. Parasites of various ages were present in all. The smallest were minute rings. Intermediate stages were round, oval, or irregular in shape, and about 3–4 μ long. Developing schizonts were small, round bodies; some, 2·5 μ in diameter, had two nuclei and scattered, fine, round grains of pigment; slightly larger ones were 3·5 μ in diameter, with four nuclei; and those with more than four nuclei usually had the pigment clumped into a single mass. The mature schizonts were about 5 μ in diameter, and had from 8 to 12 merozoites, each appearing as a reddish ring, as if the chromatin were dispersed around the rim. The gametocytes measured 5–7 μ by 4–6 μ. Macrogametocytes stained blue, with fairly dense central nucleus surrounded by a halo. Microgametocytes were paler, with larger, more diffuse nucleus. Scattered, round grains of pigment were present, sometimes aggregated in the female gametocytes into two or three larger masses.



Figs. 18–27.—*Plasmodium relictum* in *Passer domesticus*: 18, ring; 19, amoeboid; 20–23, developing schizonts; 24, almost mature schizont; 25, very small schizont; 26, macrogametocyte; 27, microgametocyte.

Life History

Lawrence (1946) showed that *Culex fatigans* Wied. was a good host in Sydney. The mosquitoes fed readily on sparrows, and 70 per cent. of those that fed became infected.

PLASMODIUM sp.

Breinl (1913) reported finding *Proteosoma praecox* in a *Falco hypoleucus* Gould, found dying by the roadside in the Lower Burdekin district, N. Qld. Young rings, amoeboids, schizonts, and gametocytes were present. Usually 18–24 merozoites were formed. The female gametocytes were bean- or sausage-shaped, with dark blue cytoplasm, dense central nucleus, and a few dark pigment granules. The male gametocytes stained a light bluish colour with an open meshwork nucleus, and coarse pigment. The host cell nucleus was usually displaced. Up to four young trophozoites were observed in a cell.

This description and Breinl's figures could fit some strains of *P. relictum*, but the pigment appears to be much coarser and darker than in the parasite of sparrows in Australia, and many more merozoites were formed than in the infections of sparrows seen by us. Coatney and Roudabush (1949) did not list a *Plasmodium* in falcons or related birds, so that a new name may have to be proposed for this parasite, when more material is available.

PLASMODIUM sp.

Mr. A. J. Bearup (personal communication) has found *Plasmodium* sp. in a *Larus novae-hollandiae* Stephens at Sydney. The parasites were shown to develop in *Culex fatigans*.

Genus HAEMOPROTEUS Kruse*

Studies of *Haemoproteus* are not very advanced. Many species have been described, but their validity is rarely well established, and the life histories of only a few have been worked out. The parasites seen in the peripheral blood are gametocytes, so that subinoculation experiments with these forms are valueless. Exoerythrocytic schizogony has been observed in other parts of the world in several species: in pigeons, in a kestrel, in a swallow, and in Bagdad sparrows. Schizonts were of considerable size, up to 60 μ, and of irregular shape, within the endothelial cells of capillaries of various organs, particularly the lungs. They were readily found at the end of the incubation period, when gametocytes were just beginning to appear in the circulation.

H. columbae of pigeons has been shown by many observers to be transmitted by hippoboscid flies, transmission by *Pseudolynchia canariensis* (Macq.) (syn. *Lynchia maura* Bigot) being recorded by Sergent and Sergent as early as 1906. Details of the development to the ookinete stage were frequently observed, but many workers failed to trace the parasite any further, although the flies certainly became infective. Adie (1915) described oocyst formation on the midgut, development of sporozoites, and their migration to the salivary glands, just as in malaria parasites in mosquitoes. The discovery by Tarshis (1953) of oocyst-like bodies on the gut of newly emerged (and unfed) hippoboscid flies threw doubt on the details of Adie's observation, but it is certain that sporozoites invade the salivary glands of the fly.

Clinically, there may be an acute phase, with many parasites in the blood, followed by a chronic phase, which has been shown to last for three years in some sparrows and pigeons. Parasites may disappear for a time, and then reappear.

Most infections studied in Australian birds have been in the chronic phase, with scanty gametocytes in the blood, and workers in this country have been puzzled as to the specificity of the numerous strains of *Haemoproteus* found. Cleland

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* The synonym *Halteridium* Labbé, 1894, has given a convenient common name, "halteridium", for the characteristically shaped parasites of birds.

and Johnston gave five specific names to parasites of native birds, but Breinl (1913) used the names applied to parasites of European birds, *H. columbae* for those of the purple-crowned fruit pigeon, and *H. noctuae* for those of the boobook owl. He tentatively placed under *H. danilewskii* the parasites seen in an eagle, a heron, and several passerine birds, noting that further study was necessary to decide whether they were the same species, or whether they should be regarded as specific for the different hosts. Unfortunately, the position is scarcely any clearer now than it was 48 years ago.

Coatney (1936) listed 31 bird parasites belonging to *Haemoproteus*, including the five species described by Cleland and Johnston, and many more have been named since. In 1938, Coatney and West redescribed *H. danilewskii* Kruse, 1890, from the crow, *Corvus brachyrhynchos*, and it appears that this specific name should now be reserved for parasites of Corvidae.

Morphological studies alone are inadequate in deciding specificity, as great variation in size, shape, arrangement of the pigment, and effect on the host cell may be seen in one film. The time elapsing between the death of the host and making the film may be very important. If parasites have begun to round up in preparation for exflagellation and fertilization, their appearance will be completely altered, and the appearance of the host cell and the amount of displacement of its nucleus will also be altered. The amount of pigment depends partly on the age of the parasite, young forms having less than older ones. The size and shape of the individual grains may also be a function of age, pigment being fine and scattered in the young forms, and tending to clump in the mature gametocytes.

In view of these difficulties, we have provisionally accepted the names already established as valid, and refrained from proposing any new ones.

HAEMOPROTEUS COLUMBAE Kruse

Haemoproteus columbae Kruse, 1890, p. 370.

Australian hosts.—*Columba livia* Gmelin, *Ptilinopus superbus* (Temminck).

Australian distribution.—Western Australia; Townsville, Qld.

The type host for this species is the common pigeon, *Columba livia*, which has a wide distribution in Europe, Africa, and Asia, and has been introduced into many parts of Australia, being common in most cities.

Wenyon (1926) stated that multiple infection of red cells with minute rings, which are the very young gametocytes, was common, but it was rare to see more than one mature gametocyte in a cell, so that those cells with multiple infection must die, or some of the parasites must leave the cell. When fully formed, the elongate, sausage-shaped gametocyte sometimes encircled the red cell nucleus. The single nucleus was central, and pigment was distributed throughout. Male and female forms were distinguishable. In the male, pigment was frequently aggregated into a number of spherical masses, and it was more uniformly distributed in the female.

Breinl (1913) recorded a scanty infection with *H. columbae* in *Ptilinopus superbus* from Townsville. The parasites were up to 15 μ in length by 6 μ in width.

The nucleus was usually central, and the pigment occurred in variable amounts of dark brownish or black granules. Male and female forms were observed. Films were made from the internal organs, but schizonts were not seen. Breinl remarked that this was probably because the bird was in the chronic stage of infection. Scott (1927) recorded an infection in the same species in the London Zoological Gardens.

We have seen a rather scanty infection in *C. livia* from Western Australia. The gametocytes measured from 13 to 15 μ by 4 to 4·5 μ. They displaced the host cell nucleus laterally, but did not encircle the ends of it. The infected red cells were slightly enlarged.

HAEMOPROTEUS NOCTUAE Celli & San Felice

Haemoproteus noctuae Celli and San Felice, 1891 (page number not available).

Australian hosts.—*Ninox novae-seelandiae* (Gmelin), *N. strenua* (Gould).

Australian distribution.—Brisbane, Eidsvold, Townsville, Qld.

We have followed Breinl (1913) in tentatively placing the parasites of Australian owls under this species, which was originally described from the little owl, *Athene noctua*, in Europe.

Cleland and Johnston (1910) described and figured, but did not name, halteridia from an owl, *Ninox* sp., taken near Brisbane by Dr. T. L. Bancroft. The parasites were relatively abundant, and male and female forms were recognized. The figures show small, elongate to plump, sausage-shaped parasites. The largest did not fill the red cell, which appeared to be enlarged. The host cell nucleus was slightly displaced laterally. Pigment occurred as fine to coarse granules, with a tendency to be grouped at the poles. Breinl (1913) recorded *H. noctuae* from *N. novae-seelandiae* at Townsville, and Cleland (1915) recorded similar parasites in *N. novae-seelandiae* and *N. strenua* from Eidsvold.

HAEMOPROTEUS NETTIONIS (Johnston & Cleland)

Halteridium nettionis Johnston and Cleland, 1909, p. 503.
Haemoproteus nettionis (Johnston and Cleland), Coatney, 1936, p. 89.

Australian hosts.—*Anas castanea* (Eyton), *Anas superciliosa* (Gmelin), *Casarca tadornoides* (Jardine & Selby).

Australian distribution.—New South Wales; Brisbane.

This species was described from a film made by Dr. F. Tidswell in 1907. A scanty infection was present in 1 out of 2 chestnut teals examined. The host was originally known as *Nettion castaneum*, hence the specific name of the parasite.

Morphology (Plate 3, Fig. 4)

The authors described male and female gametocytes. The male cells had pale cytoplasm, and large pigment granules, usually fairly evenly distributed, or tending to form groups. The female cells were more deeply stained, with smaller, but more numerous pigment granules, usually evenly distributed, but sometimes in groups. The nucleus of the host cell was usually displaced laterally. The parasites measured 18 μ along the mid-line by 4 μ in width. This parasite differed from those described from passerine birds in its larger size, and more numerous and larger pigment granules. We have seen very scanty infections in 2 out of 77 black ducks examined. Plimmer (1912) reported as *H. danilewskii* the parasites found in a *Casarca tadornoides* dying in the London Zoological Gardens.

Life History

The same species of *Haemoproteus* has been found in several species of ducks and geese in North America (Herman 1954), and the life history has been worked out by Fallis and Wood (1957) in Canada. During their studies on *Leucocytozoon* infections, they observed that *Haemoproteus* was also being transmitted to clean domestic ducks exposed to the bites of various biting flies. They found that ducks exposed at night became infected with *Haemoproteus*, whereas those exposed by day and protected at night did not. This was the reverse of what happened with *Leucocytozoon*, which was being transmitted by day-biting blackflies. Eventually they were able to demonstrate that certain biting midges, *Culicoides* sp., acted as vectors. Ookinetes and structures which were interpreted as oocysts were found, and sporozoites were seen in sections of midges. The prepatent period in the duck was 14–21 days. Hippoboscid flies were not found on any of the ducks examined.

HAEMOPROTEUS PTILOTIS (Cleland & Johnston)

Halteridium ptilotis Cleland and Johnston, 1909, p. 77.
Haemoproteus ptilotis (Cleland and Johnston), Coatney, 1936, p. 89.

Hosts.—*Meliphaga chrysops* (Latham), *M. fusca* Gould, *M. plumula* (Gould), *M. penicillata* Gould, *M. virescens* (Vieillot), *M. melanops* (Latham).

Distribution.—Milson I. (type locality), N.S.W.; Perth; Blanchetown, Beltana, Murray R., S. Aust.; Eidsvold, Qld.

The type host was previously known as *Ptilotis chrysops*, hence the specific name of the parasite.

Morphology

The gametocytes were seen in several stages of growth. The smallest lay alongside the nucleus as a curved, sausage-shaped body, the largest encircled the nucleus at each end. Only very slight displacement of the nucleus was seen in a few examples. The pigment usually occurred in coarse masses, with a tendency to be grouped at each end. This was particularly noticeable in the male gametocytes, in two of which the granules were rod-shaped. The parasites measured 9–13 μ by 2–2·5 μ.

Cleland and Johnston (1910) recorded halteridia in *M. plumula* from Perth, stating that they could find no differences between the parasites in it and in *M. chrysops* from Milson I. except in a smaller amount of pigment. In 1911, Cleland and Johnston recorded halteridia in the blood of 3 out of 9 specimens of *M. fusca* obtained in Eidsvold, and the only specimen of *M. virescens* (syn. *Ptilotis sonorus*) obtained at Blanchetown, S. Aust. While they did not apply the specific name *ptilotis* to either of them, they did not mention any differences from that species.

In 1915, Cleland recorded *Haemoproteus* in *M. penicillata* (syn. *leilavalensis*) from the Murray R., and in 1922 from Beltana, S. Aust. Plimmer (1915) recorded an infection in *M. melanops* (syn. *auricomis*) in the London Zoological Gardens.

HAEMOPROTEUS PHILEMON (Cleland & Johnston)

Halteridium philemon Cleland and Johnston, 1909, p. 81.
Haemoproteus philemon (Cleland and Johnston), Coatney, 1936, p. 89.

Host.—*Philemon corniculatus* (Latham).

Distribution.—Milson I. (type locality), Glen Davis, Cobark, Myall Lakes, N.S.W.; Eidsvold, Townsville, Qld.

Morphology (Plate 3, Fig. 5)

In the bird from Milson I., the earliest stages appeared as small, elongate bodies, usually lying lateral to the nucleus of the red cell. Fine granules of pigment were present along the side of the parasite next to the nucleus, or scattered irregularly, or clumped at the ends. The mature gametocyte tended to curl around the nucleus at each end. The authors stated that the largest forms seen seemed to be larger than those of *H. ptilotis*, and they concluded by saying " . . . the identity or otherwise of the two must await investigation of other stages in their life-histories."

Cleland and Johnston (1911) recorded this species in 1 out of 2 birds obtained at Eidsvold, but did not add anything to their original description. Breinl (1913) recorded parasites as *Haemoproteus danilewskii* from a friar bird from Townsville. His figure shows an organism very like those described above.

We have seen three moderate infections, one in a bird from Myall Lakes, and two in slides sent to us by the Rev. R. Palmer from Glen Davis and Cobark. The parasites varied from small, elongate bodies lying alongside the host cell nucleus to typical forms filling one side and both ends of the cell. Quite frequently, rounded forms were seen, which distorted the red cell, and displaced its nucleus. Pigment was present, usually as a few, large, irregular granules in the largest forms (Plate 3, Fig. 5). Mr. Palmer also preserved pieces of heart, liver, and lung, but no schizonts were found in sections of these organs.

HAEMOPROTEUS MELIORNIS (Cleland & Johnston)

Halteridium meliornis Cleland and Johnston, 1909, p. 90.
Haemoproteus meliornis (Cleland and Johnston), Coatney, 1936, p. 89.

Host.—*Meliornis novae-hollandiae* (Latham).

Distribution.—Sydney.

Morphology

The infection was apparently in an early stage, because the majority of parasites seen were young forms. These young parasites were present in about 20 per cent. of the red cells, and frequently 2 to 4 were seen in a single cell, the maximum number found being 7. They were irregular, faintly staining, amoeboid bodies, situated in various parts of the cell. Some halteridium-like forms were seen, which tended to curl round the ends of the nucleus of the red cell. These had an irregular, ill-defined outline, unlike the halteridia seen in other birds. They measured 12–14 μ by 2 μ. They contained only a few granules of pigment, usually aggregated towards one end. The authors at first thought that they were dealing with a *Plasmodium*, but the presence of small parasites in other *Haemoproteus* infections (*H. ptilotis* and *H. philemon*) and the shape of the largest parasites in *Meliornis* led them to identify it as a halteridium.

Haemoproteus in other Honeyeaters

Three specific names are available for the parasites of honeyeaters, *H. ptilotis* being the first one proposed. The parasites of all species belonging to the genus *Meliphaga* have been tentatively allotted to this species, and it is possible that *H. meliornis* and *H. philemon* may prove to be synonyms of it. Meanwhile, it is difficult to know how to place the following forms listed from other honeyeaters, but they probably belong in the same complex.

(1) *Haemoproteus* from *Melithreptus lunatus* (Vieillot) (syn. *atricapilla*), *M. validirostris* (Gould), and *M. brevirostris* (Vigors & Horsfield): Cleland and Johnston (1910) recorded halteridia in *M. lunatus* obtained near Sydney. The parasites were rather large, but did not displace the host nucleus. The parasite nucleus was either narrowly elongate or rounded, and placed centrally or nearly so. The figure shows the pigment as rounded granules of various sizes, often with a polar distribution. Cleland (1915) recorded scanty halteridia in *M. validirostris* from Flinders I., Bass Strait, remarking on the scarcity of pigment, even in the largest forms, and in 1922 he recorded parasites in *M. brevirostris* taken near Encounter Bay, S. Aust.

(2) *Haemoproteus* from *Myzomela sanguinolenta* (Latham): Cleland and Johnston (1911) recorded halteridia in 1 out of 4 specimens obtained at Eidsvold. The parasites occupied one side and the ends of the host cell, and had fairly abundant, coarse pigment. In 1915, Cleland studied an abundant infection from the same locality. The parasites occupied nearly all the host cell, and had a few large grains of pigment.

(3) *Haemoproteus* from *Myzantha melanocephala* (Latham) (syn. *garrula*), and *M. flavigula* Gould: Cleland and Johnston (1911) recorded halteridia in *M. melanocephala* from Eidsvold and *M. flavigula* from Rowena, N.S.W. In the latter, pigment was present in fairly large rods.

(4) *Haemoproteus* from *Acanthagenys rufogularis* Gould: Cleland (1915) recorded halteridia in birds from Cobar and from Merrool, near Yanco, N.S.W., and in 1922 recorded another infection from a bird taken at Narrabri, N.S.W. In this film, only a single parasite was seen, occupying a side and both ends of the red cell.

(5) *Haemoproteus* from *Entomyzon cyanotis* (Latham): Cleland and Johnston (1911) recorded a few halteridia in 1 out of 7 birds from Eidsvold.

(6) Breinl (1913) recorded as *Haemoproteus danilewskii* the parasites found in *Anthochaera chrysoptera* (syn. *Anellobia chrysoptera*) at Townsville.

HAEMOPROTEUS GEOCICHLAE (Cleland & Johnston)

Halteridium geocichlae Cleland and Johnston, 1909, p. 85.
Haemoproteus geocichlae (Cleland and Johnston), Coatney, 1936, p. 88.

Host.—*Oreocincla lunulata* (Latham), previously known as *Geocichla lunulata*, hence the specific name of the parasite.

Distribution.—Bulli Pass, N.S.W.

Morphology

The authors observed numerous parasites which were free in the plasma, having apparently been liberated from the red cells during the spreading of the blood. These were rounded forms about 4 μ in diameter. From one to three young forms were seen in red cells. Mature, halter-shaped organisms measured 11–12 μ by 3 μ. Male and female forms were observed. Some rounded-up gametocytes were seen bulging the distorted host cell. A puzzling series of forms was also seen, consisting of all intermediate stages between normal halter-shaped forms and forms in which a constriction had almost divided the parasite into two rounded masses connected by a protoplasmic thread.

UNNAMED HAEMOPROTEUS FROM OTHER BIRDS

As morphological characters of value appear to be lacking in these parasites, the available information about the unidentified *Haemoproteus* of other birds is summarized in Table 1.

Genus LEUCOCYTOZOON Danilewsky

Members of this genus appear to be restricted to birds. It was at first thought that the parasites were always in white cells, hence the name given by Danilewsky. It was also thought that the lack of pigment was correlated with the absence of haemoglobin in the parasitized cell. However, doubts were soon expressed about the nature of the host cell, even by Danilewsky himself. Cleland and Johnston (1911) found very young forms definitely parasitizing red cells in a honeyeater, *Meliphaga fusca*. Wenyon (1926) considered that the youngest forms were in immature red cells. Hartman (1929) found the earliest stages of *L. anatis* (i.e. *L. simondi*) in young red cells. This has been confirmed recently by the development of a specific stain for haemoglobin, which can be used in conjunction with the Romanowsky method (Ralph 1941). By this method, Cook (1954) clearly showed that the growing forms of *L. simondi* were in red cells. By the time the gametocytes were full-grown, they had replaced the host cell cytoplasm entirely, and no reaction for haemoglobin was obtained. This organism, then, can metabolize the cell protoplasm without the production of pigment, which is such a characteristic feature of species of *Plasmodium* and *Haemoproteus*. However, some species may parasitize white cells. Levine (1954) considered that the young gametocytes of *L. marchouxi* in doves were in lymphocytes.

Wenyon (1926), studying *L. neavei* in the guinea-fowl, noted that the living parasite was very active, waves of peristalsis passing in either direction, and forcing the cytoplasm of the parasite out into the spindle-like extremities of the host cell. He also noted that, although in a wet preparation all the parasites were in spindle-shaped cells, in dried film many were in round cells, and the horn-like prolongations had disappeared. This indicates that classifying members of this genus according to whether they are in round or elongate cells is of doubtful value.

TABLE 1

UNIDENTIFIED HAEMOPROTEUS FROM VARIOUS BIRDS

Host	Authority	Locality	Number Examined	Number Infected	Remarks
Alectura lathami	Cleland and Johnston (1911)	Eidsvold, Qld.	7	6	
	Cleland (1915)	Eidsvold	1	1	
	This paper	Eidsvold	4	3	
Eupodotis australis	This paper	Mitchell R., Qld.	2	1	Plate 3, Fig. 6
Notophoyx novae-hollandiae	Breinl (1913)	Townsville, Qld.	6	1	As *danilewskii*
Haliastur indus	Breinl (1913)	Townsville	1	1	As *danilewskii*
Podargus strigoides	This paper	Eidsvold		1	
Platycercus adelaidae	Cleland and Johnston (1911)	Adelaide	1	1	
Kakatoë galerita	This paper	Theodore, Qld.	25	3	
Dacelo gigas	Johnston (1910)	Sydney	1	1	
	Welsh and Priestley (1911)	Sydney	1	1	Numerous in sick bird
Merops ornatus	Cleland and Johnston (1911)	Eidsvold	5	2	
Eudynamys orientalis	Breinl (1913)	Townsville		1	As *danilewskii*
	Cleland (1922)	Casino, N.S.W.	2	2	
Microeca fascinans	Cleland and Johnston (1911)	Eidsvold	10	8	
Petroica phoenicea	Cleland and Johnston (1911)	Mt. Kosciusko, N.S.W.	1	1	Very little pigment
Myiagra ?rubecula	Cleland and Johnston (1910)	Hawkesbury R., N.S.W.	1	1	
Pomatostomus superciliosus	Cleland and Johnston (1910)	Adelaide	3	1	
Gerygone olivacea	Cleland (1915)	Molong, N.S.W.	1	1	
Megalurus gramineus	Breinl (1913)	Townsville		1	As *danilewskii*
Grallina cyanoleuca	Cleland and Johnston (1911)	Eidsvold	2	1	10 per cent. of cells infected
	This paper	Mornington I., Qld.	5	1	Plate 3, Fig. 7

TABLE 1 (*Continued*)

Host	Authority	Locality	Number Examined	Number Infected	Remarks
Gymnorhina tibicen	This paper	Brisbane	1	1	R. Palmer coll.
	This paper	Crookwell, N.S.W.	1	1	
G. hypoleuca	Plimmer (1912)	Died, London Zoo		1	As *danilewskii*
Cracticus torquatus	Breinl (1913)	Townsville		1	As *danilewskii*
Strepera graculina	This paper	Myall Lakes, N.S.W.	1	1	Plate 3, Fig. 9
Aphelocephala leucopsis	Cleland and Johnston (1911)	Blanchetown, S. Aust.	1	1	Pigment coarse
Zosterops lateralis	Cleland and Johnston (1910)	Sydney	13	3	
	Cleland and Johnston (1911)	Adelaide	1	1	
	Cleland and Johnston (1911)	Eidsvold	1	1	
	Lawrence (1946)	Sydney	3	1	
Dicaeum hirundinaceum	Cleland (1915)	Hawkesbury R.	1	1	
Pardalotus melanocephalus	Cleland and Johnston (1911)	Eidsvold	14	6	
Oriolus sagittatus	Cleland and Johnston (1911)	Eidsvold	5	3	
Chibia bracteata	Breinl (1913)	Townsville		1	As *danilewskii*
Ptilonorhynchus violaceus	Wenyon (1926)	Died, London Zoo		1	
	This paper	Dorrigo, N.S.W.	1	1	Plate 3, Fig. 8 R. Palmer coll.
Chlamydera nuchalis	Breinl (1913)	Townsville	5	1	As *danilewskii*

Life History

Exflagellation and ookinete formation were observed by Danilewsky, and confirmed by many others. O'Roke (1934) first proved that *L. simondi* of ducks was transmitted by blackflies (Simuliidae). Huff (1942) showed that there were two exo-erythrocytic cycles in the duck, one producing small schizonts in liver cells, and one producing megaloschizonts in the spleen and other organs of the reticulo-endothelial system.

Recently Fallis, Davies, and Vickers (1951) and Fallis, Anderson, and Bennett (1956) have worked out the details of sporogony in the blackfly and schizogony in the duck. A striking feature is the rapidity with which each cycle is completed. Sporozoites may be present in a blackfly 72 hr after an infective feed, and gametocytes may appear in the blood of the duck 6 days after exposure to blackflies.

Infected ducks may show splenomegaly and anaemia, which may be fatal. Ducks, which recover from the acute phase, may show scanty parasites, or an intermittent parasitaemia, for months.

Taxonomy

Coatney (1937) listed 59 species from birds, some of which are regarded as synonyms. There are few, if any morphological differences between the species. All possess sharply vacuolated cytoplasm, which stains blue, and an oval or round nucleus, which stains red with Romanowsky stains. All have the property of causing enlargement and distortion of the host cell and its nucleus, which is usually drawn out into a narrow band more or less encircling the parasite. However, there are definite indications of host-specificity. Thus Fallis, Pearson, and Bennett (1954) found that *L. simondi* was transmitted naturally to domestic ducks and geese in Canada, but not to turkeys, chickens, grouse, or pheasants exposed alongside them.

Nearly all the infections seen by us had reached the chronic phase, with scanty parasites. They were usually in oval or rounded cells, but we have not had the opportunity to observe them alive. We have attempted to meet an impossible taxonomic situation by allotting the parasites found in several honeyeaters to *L. anellobiae* Johnston, 1912, and using specific names given to parasites of related birds in other parts of the world for the forms seen in an owl, a cormorant, a frogmouth, and a mutton-bird.

Although there do not appear to be useful morphological characters, we have given the size of the parasite and effect on the host cell, when these facts are available.

LEUCOCYTOZOON VANDENBRANDENI Rodhain

Leucocytozoon vandenbrandeni Rodhain, 1931, p. 276.

Australian host.—Phalacrocorax melanoleucus (Vieillot).

Australian distribution.—Mildura, Vic.

Rodhain (1931) described this species from a cormorant, *Plotus rufus*, from Leopoldville, Belgian Congo. He evidently considered it an uncommon parasite, as he stated that he had examined the blood of pelicans and cormorants in 1911 and 1912 without finding any parasites.

The parasites measured up to 16 μ in diameter, with a large nucleus. The microgametocytes were slightly smaller. The smallest parasite seen was 4 by 1 μ. The host cell nucleus was distorted into a filament. Double and even triple infections were seen.

We have seen rather scanty infections in 6 out of 35 *P. melanoleucus* taken on the Murray R. below Mildura. Five of the infected birds were juveniles. All the parasites stained a deep blue colour, and were presumably macrogametocytes. They measured about 11 by 10 μ, some slightly elongate forms being 15 by 9 μ. The nucleus of the host cell was enlarged and compressed into a narrow oval, but was not drawn out into the long, ribbon-like structure seen in some other birds (Plate 4, Fig. 1).

LEUCOCYTOZOON DANILEWSKYI Ziemann

Leucocytozoon danilewskyi Ziemann, 1898 (page not available).

Australian host.—Ninox novae-seelandiae (Gmelin).

Australian distribution.—Myall Lakes, N.S.W.

Sambon (1908) stated that Ziemann gave the above name to a parasite of the little owl, *Athene noctua*, in Italy; he considered *ziemanni* Laveran, 1902, to be a synonym. The parasites were in both spindle-shaped and round cells, and free macrogametocytes measured 8–12 μ in diameter, with a round or elongate, central nucleus. The microgametocytes were slightly smaller, with pale greyish cytoplasm, and a large, diffuse nucleus. The microgametes were 20–30 μ in length.

We have seen what is possibly the same species in *N. novae-seelandiae* from Myall Lakes. The parasites were oval or round, and varied from 15 by 9 μ up to 18 by 13 μ. The nucleus of the host cell was compressed and elongated, but not usually encircling the parasites (Plate 4, Fig. 2).

LEUCOCYTOZOON CAPRIMULGI Kerandel

Leucocytozoon caprimulgi Kerandel, 1913, p. 438.

Australian host.—Podargus strigoides (Latham).

Australian distribution.—Eidsvold, Qld.

Kerandel described this species from a night-jar, *Caprimulgus fossei*, from the French Congo. Oval forms in fusiform cells measured 16–18 μ by 6–8 μ; in round cells, the measurements were 12–16 μ by 7–11 μ. The microgametocytes had a large, oval nucleus occupying a considerable part of the body. There is nothing characteristic about the morphology of this species, and we have allotted the parasites of the frogmouth to it simply because of the relationship of the hosts.

Cleland (1915) recorded a moderately numerous infection in films from *P. strigoides* from Eidsvold. He recognized male and female forms, measuring from 8·5–10·5 μ in diameter. We have seen a scanty infection in the same species from the same locality. The parasites were small, about 5 or 6 μ in diameter, and some were clearly in red cells, others free in the plasma.

LEUCOCYTOZOON ANELLOBIAE Johnston

Leucocytozoon anellobiae Johnston, 1912, p. 110.

Hosts.—Anthochaera chrysoptera (Latham), *Acanthagenys rufogularis* Gould, *Entomyzon cyanotis* (Latham), *Meliphaga fusca* Gould, *Myzantha melanocephala* (Latham), *Myzomela sanguinolenta* (Latham), *Philemon corniculatus* (Latham).

Distribution.—Merrool, near Yanco, Bumberry, Milson I., Myall Lakes, Grafton, N.S.W.; Eidsvold, Townsville, Qld.

Morphology (Plate 4, Figs. 4 and 5)

Cleland and Johnston (1911) described the forms seen in *Anthochaera chrysoptera* (syn. *Anellobia chrysoptera*), which should be regarded as the type host. They were more or less globular parasites, embayed in the nucleus of the host cell. Usually they were deeply stained, but occasionally paler forms were found. At that time, these parasites were regarded as intracorpuscular trypanosomes, and included under the name *Trypanosoma anellobiae.* The authors also recorded similar parasites from Eidsvold in all the birds listed above, with the exception of *Acanthagenys rufogularis* and *Philemon corniculatus.* A year later, Johnston used the name *Leucocytozoon anellobiae* for these parasites. He also allotted to this species parasites found in *Oriolus sagittatus*, *Sphecotheres vieilloti*, and *Corcorax melanorhamphus.* However, these are all probably distinct from the parasites of the Meliphagidae.

Breinl (1913) recorded *Leucocytozoon* in *Philemon corniculatus* from Townsville, and Cleland (1915) added *Acanthagenys rufogularis* from Yanco to the host list. We have seen *L. anellobiae* in several species of honeyeaters from Eidsvold, and in 1 out of 3 *A. chrysoptera*, in 1 out of 3 *M. melanocephala*, and in a specimen of *P. corniculatus* from Myall Lakes. In the last, the parasites measured from 10 by 7 μ up to 13·5 by 8 μ. The nuclei of the macrogametocytes were compact (Plate 4, Fig. 5), and sometimes divided into two or three separate portions; those of the microgametocytes were diffuse, occupying about one-half of the parasite (Plate 4, Fig. 4). The nucleus of the host cell usually encircled from one-quarter to one-half of the parasite.

LEUCOCYTOZOON SAKHAROFFI Sambon

Leucocytozoon sakharoffi Sambon, 1908, p. 325.

Australian host.—*Corcorax melanorhamphus* (Vieillot).

Australian distribution.—Glen Davis, N.S.W.; Eidsvold, Qld.

Sambon (1908) described this species from a raven, *Corvus corax*, from Europe. The parasites were usually round. The cytoplasm of the macrogametocytes was granular, staining an intense blue colour, and presenting numerous minute vacuoles; the nucleus was light pink, with indistinct contour. The cytoplasm of the microgametocytes was hyaline, greyish; their nuclei were not always clearly visible, and were sometimes broken up into filaments or granules. The nucleus of the host cell surrounded the parasite almost entirely.

Cleland and Johnston (1911) recorded and figured, but did not name, parasites in 2 out of 6 *C. melanorhamphus* from Eidsvold. Johnston (1912) placed them as *L. anellobiae.* However, they are probably more nearly allied to the above species from another corvine bird.

We have seen a scanty infection in films sent by the Rev. R. Palmer, from Glen Davis. One free macrogametocyte measured 13 by 11 μ. The nucleus of the host cell was sometimes drawn out into a long, narrow ribbon, enclosing the parasite for three-quarters of its circumference (Plate 4, Fig. 3).

UNNAMED LEUCOCYTOZOON FROM AUSTRALIAN BIRDS

As with *Haemoproteus*, it is convenient to present the available information about infections in other species of birds in tabular form (Table 2).

Genus LANKESTERELLA Labbé

Synonym *Atoxoplasma* Garnham.

As well as the large, easily recognizable parasites belonging to the genus *Leucocytozoon*, there are other unpigmented parasites, which appear to be less common. They may be divided into three groups.

The first group includes small, erythrocytic parasites allied to piroplasms. Laird and Lari (1957) redescribed *Babesia moshkovskii* (Schurenkova) from an Indian crow, reviewing the literature dealing with it, and with the better known *Aegyptianella pullorum* Carpano, a parasite of fowls and many other birds. No member of this group has yet been found in Australia.

TABLE 2

UNIDENTIFIED LEUCOCYTOZOON FROM VARIOUS BIRDS

Host	Authority	Locality	Number Examined	Number Infected	Remarks
Gymnorhina tibicen	This paper	Brisbane	1	1	Plate 4, Figs. 7, 8
	This paper	Crookwell, N.S.W.	1	1	R. Palmer coll.
Strepera graculina	This paper	Myall Lakes, N.S.W.	1	1	Plate 4, Fig. 9
Climacteris picumnus	This paper	Glen Davis, N.S.W.	2	1	Plate 4, Fig. 6 R. Palmer coll.
Pardalotus melanocephalus	Cleland and Johnston (1911)	Eidsvold, Qld.	14	1	
Oriolus sagittatus	Cleland and Johnston (1911)	Eidsvold	5	3	
Sphecotheres vieilloti	Cleland and Johnston (1911)	Eidsvold	5	2	
	This paper	Brisbane	3	3	Plate 4, Fig. 10
Ptilonorhynchus violaceus	Wenyon (1926)	Died, London Zoo		1	
	This paper	Dorrigo	1	1	Plate 4, Fig. 11 R. Palmer coll.
Ailuroedus crassirostris	Cleland (1922)	Bunya Mts., Qld.	1	1	

The second group includes larger parasites, found in red or white cells, and similar to the haemogregarines of other vertebrates. Aragão (1911) described several from the white cells of South American birds. Hoare (1924) described *Hepatozoon adiei* from the monocytes of an Indian eagle. These were stout, sausage-shaped parasites, very similar in appearance to *Hepatozoon muris* (Balfour) of rats. Schizonts were found in the lungs, but the sporogony is unknown, and it is not certain, therefore, that the parasites really belong to the genus *Hepatozoon*.

The third group includes the small, ill-defined parasites of monocytes, which were formerly confused with *Toxoplasma*. Garnham (1950) proposed the genus

Atoxoplasma for them, but Lainson (1959) has worked out the life history of the species that occurs in English sparrows, and has shown that it belongs to the genus *Lankesterella*, under which *Atoxoplasma* now falls as a synonym.

True *Toxoplasma* has been found in an Australian crow, *Corvus coronoides* Vigors & Horsfield, by Cook, Pope, and Scott (1959), but the organisms recorded as *Toxoplasma* by Lawrence (1946) should be referred to *Lankesterella*, as well as those described from *Zosterops* by Laird (1950, 1959). We have also included a new erythrocytic haemogregarine provisionally in *Lankesterella*, because Baker, Lainson, and Killick-Kendrick (1959) described somewhat similar stages in *L. corvi* in the English rook. Its appearance, however, is very different from that of "*Atoxoplasma*", and it may well be that two different genera occur in birds.

LANKESTERELLA PICUMNI, sp.nov.

Host.—*Climacteris picumnus* Temminck.

Distribution.—Glen Davis, N.S.W.

Type.—Slide in the collection of the Rev. R. Palmer.

A very scanty infection was found in the red cells of a *C. picumnus* from Glen Davis. We are indebted to the Rev. R. Palmer for the films of this interesting parasite, which is the first haemogregarine-like organism to be recorded in Australian birds, and apparently the second to be recorded from the red cells of birds.

Morphology (Plate 3, Figs. 10–12)

The smallest parasite, a ring, measured 2·5 by 2 μ, and had three small chromatin masses. Larger forms were sausage-shaped, lay beside the red cell nucleus, and measured from 7 to 11 μ in length by 2 to 3 μ in breadth. One extracellular form had a fairly compact, terminal nucleus, but in the others the chromatin appeared to be dispersed in several masses. The cytoplasm was pale blue or colourless. No trace of pigment was found, and a capsule was not distinguished. The infected cells were not enlarged nor distorted in any way.

LANKESTERELLA PADDAE (Aragão)

Haemogregarina paddae Aragão, 1911, p. 55.
Atoxoplasma paddae (Aragão), Laird, 1959, p. 50.
?*Lankesterella garnhami* Lainson, 1959, p. 369.

Australian hosts.—*Passer domesticus* (L.), ?*Zosterops lateralis* (Latham).

Australian distribution.—Sydney; Brisbane.

Lainson (1959) has treated "*Atoxoplasma*" from different hosts as belonging to different species, but it is more convenient here to follow Laird (1959) in including them all under the oldest available name until more is known about them. If discrimination were needed, the name *adiei* (Aragão, 1911) would probably be the most appropriate one for parasites of sparrows, and a new name would be required for those from *Zosterops*.

Lawrence (1946) found oval, unpigmented bodies in the monocytes of sparrows in Sydney, and we have seen similar parasites in 5 out of 78 sparrows examined in Brisbane.* Laird (1950) recorded similar organisms in New Zealand, in an immigrant *Zosterops lateralis* from Australia, which might have brought its infection with it, and he identified them as *A. paddae* in 1959.

These are delicate parasites, which stain rather weakly and diffusely, and consequently are difficult to photograph satisfactorily (Plate 3, Fig. 13), but they have been clearly illustrated and described by Laird (1959). They vary from rounded bodies, about 2·5–4 μ in diameter, to oval or sausage-shaped forms up to 10 or 11 μ by 4 or 5 μ. The cytoplasm stains pale blue with Giemsa, and may contain a few granules or vacuoles; the nucleus is pink, granular, and usually shows a small, more deeply staining karyosome. The parasites tend to indent the nuclei of lymphocytes, though not of monocytes (Laird), and from one to four may be found in an infected cell.

Cleland and Johnston (1910) figured peculiar, spindle-shaped, unpigmented parasites, which they found in the plasma of *Z. lateralis*. These have not been recorded again, and they do not resemble any known parasite of birds, though they could conceivably have been distorted *Lankesterella* liberated during preparation of the slide.

VI. Acknowledgments

We would like to thank Dr. S. G. Anderson, Walter and Eliza Hall Institute, Melbourne, for the films from cormorants, Rev. R. Palmer, Crookwell, N.S.W., for many interesting blood films from birds, and Mr. A. J. Bearup, School of Public Health and Tropical Medicine, Sydney, for slides from ducks, and for permission to quote his unpublished observations on the *Plasmodium* of the silver gull.

We are indebted to Sir Edward Ford, Director, School of Public Health and Tropical Medicine, Sydney, for permission to reproduce parts of Plate VII of the First Report of the Australian Institute of Tropical Medicine, and to the Council of the Royal Society of New South Wales for permission to reproduce figures from Plates XXX and XXXI of the Journal of the Royal Society of New South Wales, Volume 45.

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* Many of the films were made from clotted blood, and contained few recognizable leucocytes, so the true incidence may have been higher.

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EXPLANATION OF PLATES 1–4

PLATE 1

Trypanosomes of Australian birds; rearranged from Breinl (1913), Plate VII. Figure 1 drawn with a $\frac{1}{12}$ in. objective and 4 × ocular; Figures 2–8 drawn with a 2 mm apochromatic objective and 8 × compensating ocular

Fig. 1.—Trypanosome in *Haliastur indus.*
Figs. 2–3.—Trypanosomes in *Falco hypoleucus.*
Figs. 4–5.—*T. chlamydoderae* in *Chlamydera nuchalis.*
Figs. 6–7.—*T. notophoyxis* in *Notophoyx novae-hollandiae.*
Fig. 8.—Trypanosome in *Ninox novae-seelandiae.*

PLATE 2

Trypanosomes of Australian birds

Figs. 1–3.—*T. ?notophoyxis* in *Demigretta sacra.*
Figs. 4–6.—*T. myzanthae* in *Myzantha melanocephala.*
Figs. 7–10.—Trypanosomes in *Meliphaga chrysops.*

PLATE 3

Sporozoan blood parasites of Australian birds

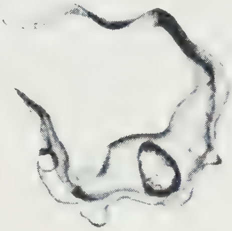
Figs. 1–3.—*Plasmodium biziurae* in *Anas superciliosa*: 1, young ring; 2, microgametocyte; 3, macrogametocyte.
Fig. 4.—*Haemoproteus nettionis* in *A. superciliosa.*
Fig. 5.—*H. philemon* in *Philemon corniculatus.*
Fig. 6.—*Haemoproteus* in *Eupodotis australis.*
Fig. 7.—*Haemoproteus* in *Grallina cyanoleuca.*
Fig. 8.—*Haemoproteus* in *Ptilonorhynchus violaceus.*
Fig. 9.—*Haemoproteus* in *Strepera graculina*, exflagellating microgametocyte.
Figs. 10–12.—*Lankesterella picumni* in *Climacteris picumnus.*
Fig. 13.—*Lankesterella paddae* in *Passer domesticus.*

PLATE 4

Leucocytozoa of Australian birds

Fig. 1.—*Leucocytozoon vandenbrandeni* in *Phalacrocorax melanoleucus.*
Fig. 2.—*L. danilewskyi* in *Ninox novae-seelandiae.*
Fig. 3.—*L. sakharoffi* in *Corcorax melanorhamphus.*
Figs. 4–5.—*L. anellobiae* in *Philemon corniculatus*: 4, microgametocyte; 5, macrogametocyte.
Fig. 6.—*Leucocytozoon* in *Climacteris picumnus.*
Figs. 7–8.—*Leucocytozoon* in *Gymnorhina tibicen.*
Fig. 9.—*Leucocytozoon* in *Strepera graculina.*
Fig. 10.—*Leucocytozoon* in *Sphecotheres vieilloti.*
Fig. 11.—*Leucocytozoon* in *Ptilonorhynchus violaceus.*

HAEMATOZOA OF AUSTRALIAN BIRDS



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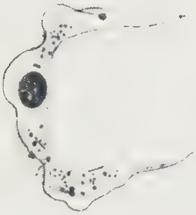

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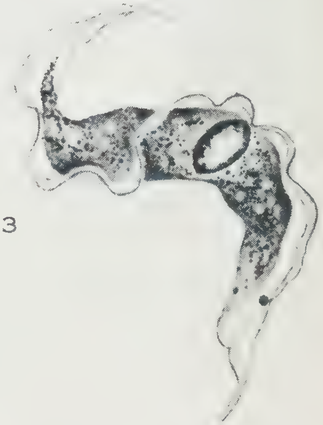

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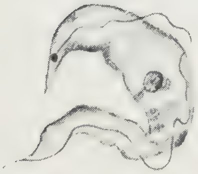

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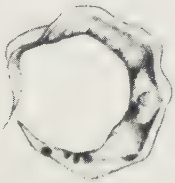

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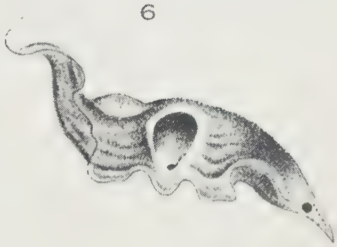

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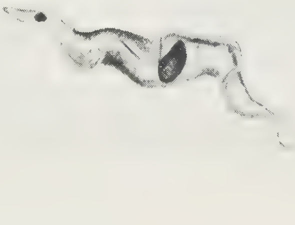

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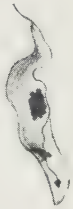

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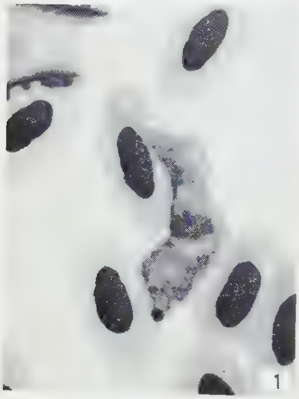
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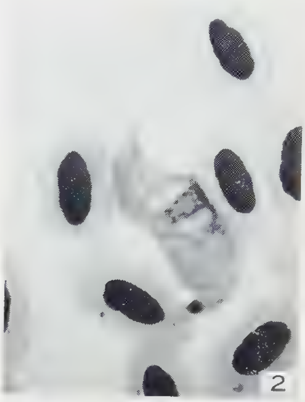
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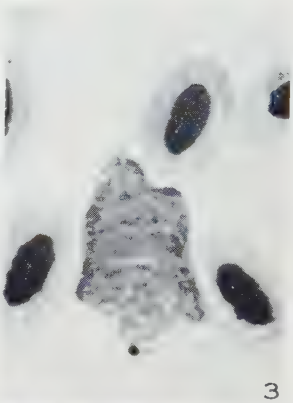
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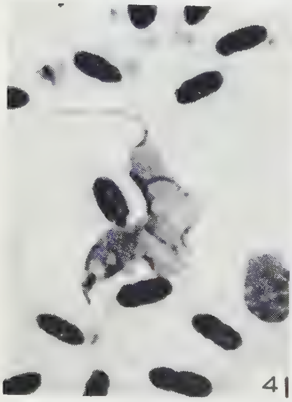
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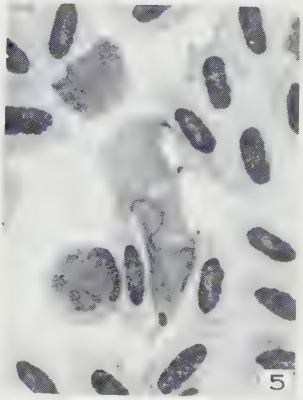
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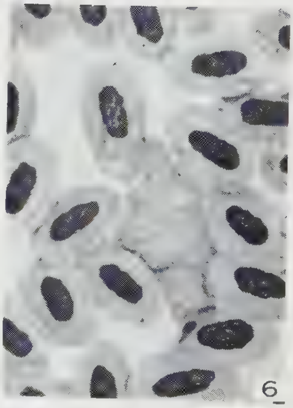
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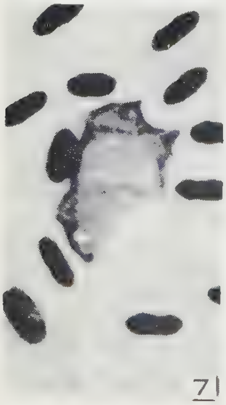
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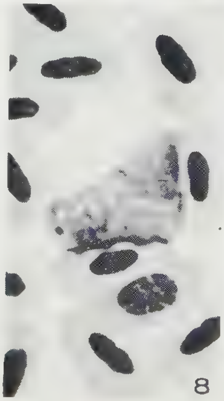
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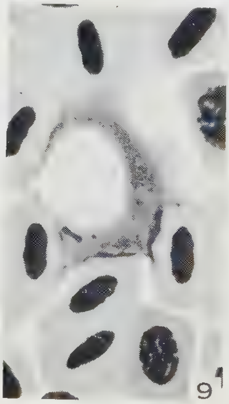
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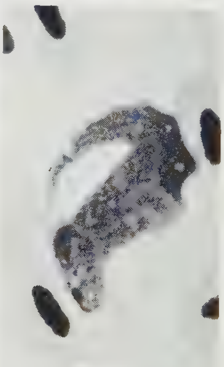

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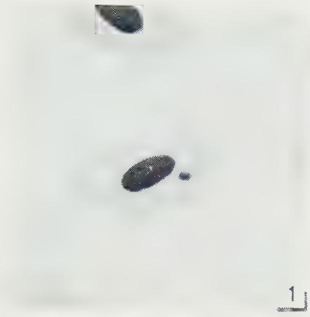
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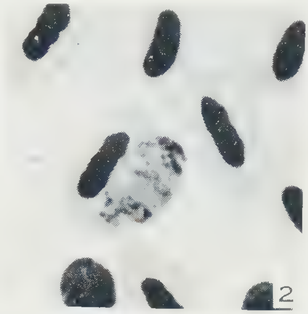
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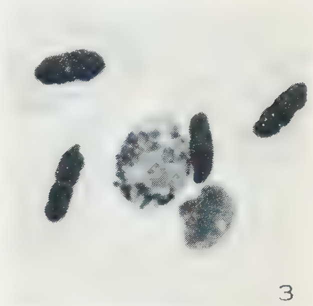
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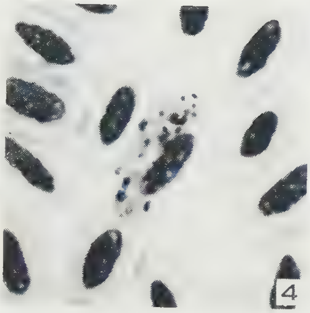
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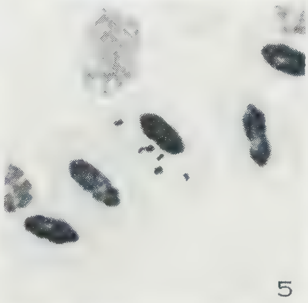
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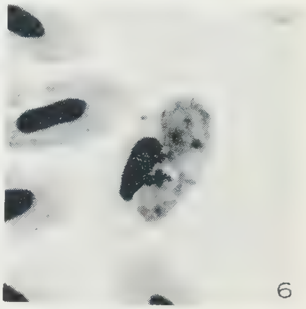
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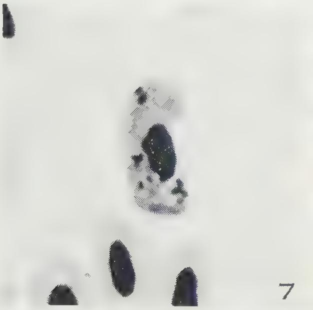
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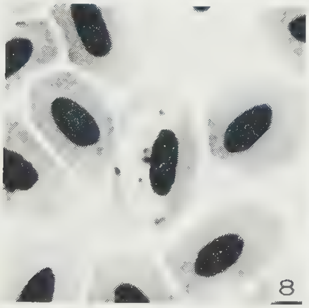
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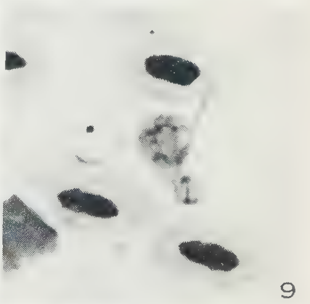
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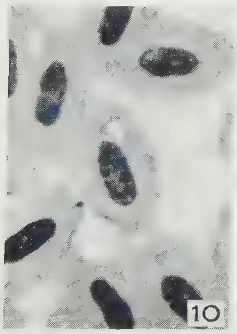
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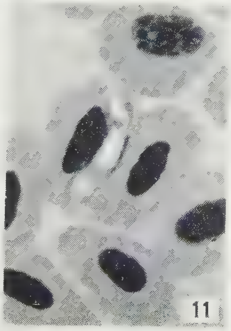
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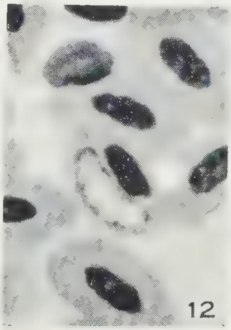
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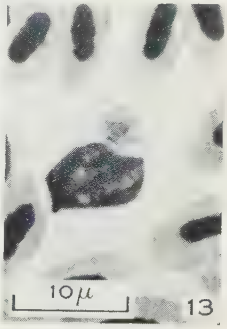

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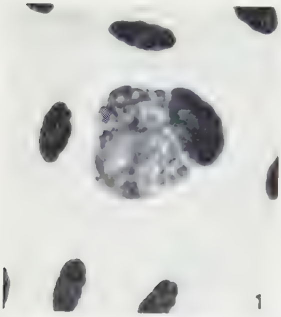
HAEMATOZOA OF AUSTRALIAN BIRDS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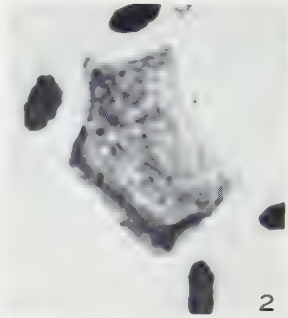
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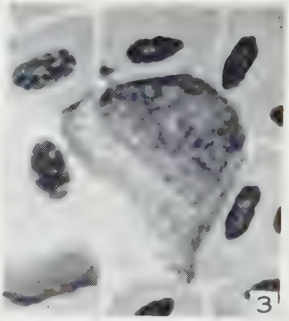
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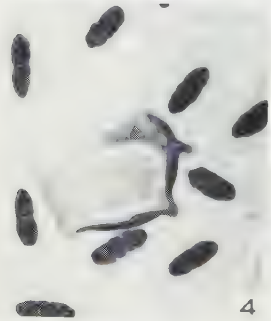
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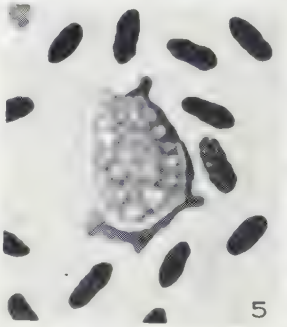
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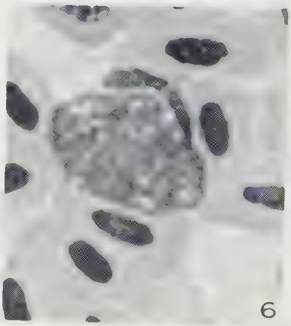
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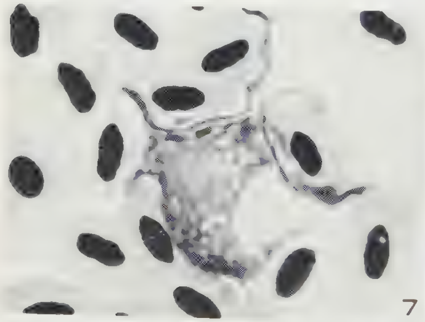
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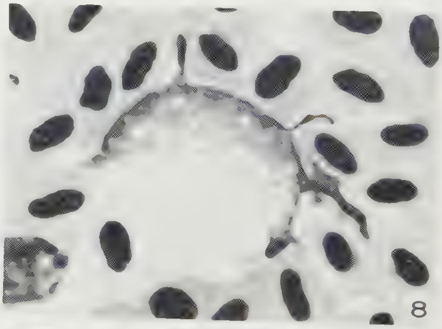
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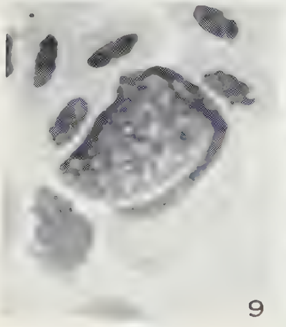
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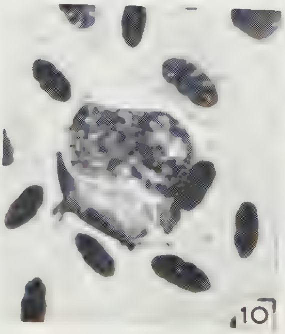
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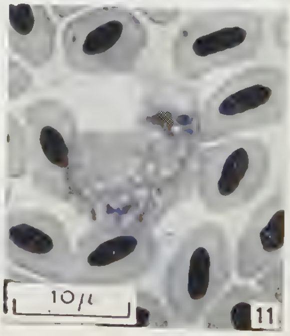

11

NEMATODES BELONGING TO THE TRICHOSTRONGYLIDAE, SUBULURIDAE, RHABDIASIDAE, AND TRICHURIDAE FROM BANDICOOTS

By Patricia M. Mawson*

[*Manuscript received January* 28, 1960]

Summary

Parasites are recorded from *Isoodon obesulus* (Shaw) (Queensland, Victoria, South Australia, and Tasmania), *I. nauticus* Thomas (South Australia), *Perameles nasuta* Geoffroy (Queensland), and *P. gunni* Gray (Tasmania). Nematode species described are:

Trichostrongylidae.—*Nicollina iota*, sp. nov.; *Austrostrongylus acinocercus*, sp. nov.; *Mackerrastrongylus peramelis* (Johnston & Mawson) (syn. *Filarinema peramelis* Johnston & Mawson); *Peramelistrongylus skedastos*, gen. et sp. nov.; *Asymmetracantha tasmaniensis*, gen. et sp. nov.

Subuluridae.—*Labiobulura peramelis* (Baylis); *L. peragale* (Johnston & Mawson); *L. baylisi*, sp. nov.; *L. inglisi*, sp. nov.

Rhabdiasidae.—*Parastrongyloides australis*, sp. nov.

Trichuridae.—*Trichurus peramelis* Baylis.

Unnamed species are *Nicollina* sp., *Austrostrongylus* sp., and *Capillaria* sp.

Notes have been given where possible on the frequency of occurrence of nematodes, and of each species of nematode, in the bandicoots. Some interesting subspecific variation in *Peramelistrongylus skedastos* and a specific variation in the species of *Labiobulura* are both linked partly with the geographical range of the host. Further work on a wider range, both geographical and specific, of bandicoots is projected.

Introduction

An attempt has been made to examine nematodes from bandicoots from as many places, and of as many species, as possible. The species already described from these hosts, and some collected but not yet described, were listed by Mackerras, Mackerras, and Sandars (1953) and M. J. Mackerras (1958). Many of the collections listed in these works have been very kindly lent to the author by Dr. M. J. Mackerras. It has not so far been possible to get fresh material from Western Australia, Northern Territory, or New South Wales. However, it has been decided to report on the numerous specimens already available (including re-examination of some specimens already recorded) and to leave a discussion of the distribution of the parasite species in relation to that of the Peramelidae until more material comes to hand.

Dr. Mackerras has provided details of collections from the Queensland bandicoots, but it is not known what was the frequency of infestation among these animals. Each of the three Tasmanian, the one Victorian, and the three South Australian bandicoots examined proved to be quite heavily infested, those from

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TABLE 1

NEMATODES RECORDED IN THIS PAPER ARRANGED TO SHOW HOSTS AND LOCALITIES

Numbers indicate the number of host animals infected with each species

Nematode	*I. obesulus*					*I. nauticus*	*P. nasuta*		*P. gunni*
	N. Qld.*	S. Qld.†	Ararat, Vic.	Cherry Gardens, S. Aust.	Dunorlan, Tas.	Nuyts I., S. Aust.	N. Qld.*	S. Qld.†	Dunorlan, Tas.
Trichostrongyles	20	18	1	2	2	—	7	4	1
Mackerrastrongylus peramelis (Johnston & Mawson)	15	5	—	—	—	—	7	1	—
Peramelistrongylus skedastos, gen. nov., sp. nov.	15	15	1	2	2	—	—	1	1
Nicollina iota, sp. nov.	2	1	—	2	2	—	4	1	—
Nicollina sp.	—	—	—	—	1	—	—	—	—
Austrostrongylus acinocercus, sp. nov.	—	—	—	—	—	—	1	—	—
Austrostrongylus sp.	—	1	—	—	—	—	—	—	—
Asymmetracantha tasmaniensis, gen. nov., sp. nov.	—	—	—	—	2	—	—	1	—
Labiobulura peramelis (Baylis)	—	1	—	—	—	—	—	—	—
Labiobulura baylisi, sp. nov.	—	3	—	—	—	—	—	—	—
Labiobulura inglisi, sp. nov.	—	—	—	3	2	1	—	—	1
Capillaria sp.	—	—	—	—	2	—	—	—	1
Trichuris peramelis Baylis	—	—	—	—	2	—	—	—	—
Parastrongyloides australis, sp. nov.	—	—	1	3	2	—	—	—	1

* Around Innisfail.

† Around Brisbane including Mt. Nebo, Mt. Glorious, and D'Aiguillar.

Tasmania particularly so; on the whole, the individuals of each species are larger from southern Australian than from Queensland hosts. To facilitate future investigation the measurements of many of the species described have been tabulated according to the place of origin. It is expected that, in answer to widely circulated requests, more material from different hosts and localities will come to hand and that a pattern of the distribution of the nematodes will emerge from this study.

The specimens from *Isoodon nauticus* Thomas are from a collection which has been in the Zoology Department, University of Adelaide, for a very long time, and, as the host species has only been recorded once, it is probable that they came from the type specimen. *I. nauticus* may be a synonym of *I. obesulus* (Shaw). Dr. Mackerras has also sent a large collection of trichostrongyles from rats collected from northern Queensland. So far these have only been examined superficially, but it is clear that they belong to species distinct from those in bandicoots, with the exception of one collection from *Hydromys chrysogaster* Geoffroy, the water rat, which consisted of specimens of the commonest trichostrongyle of bandicoots, *Peramelistrongylus skedastos*, sp. nov.

Nematodes recorded in this paper and hosts and localities are listed in Table 1. In addition, the following nematodes have been re-examined and some allotted to different hosts:

Labiobulura peragale (Johnston & Mawson) (syn. *Subulura peragale* Johnston & Mawson) from *Thalacomys minor* Spenser.

Labiobulura inglisi, sp.nov., previously assigned to *Subulura peramelis* Baylis (cf. Johnston and Mawson 1939*b*, p. 309), from *Perameles bougainvillei* Quoy & Gaimard (syn. *P. myosura*).

Labiobulura baylisi, sp. nov., previously assigned to *Subulura peramelis*, from *P. nasuta* Geoffroy (Johnston and Mawson 1939*a*, p. 204) and from *I. obesulus* (syn. *I. torosus* Ramsay) (cf. Johnston and Mawson 1951, p. 36).

Type material.—Holotype male and allotype female of new species described in this paper have been placed in the South Australian Museum; paratype material is in the Helminthological Collection, Zoology Department, University of Adelaide, and, in the case of Queensland material, in the collection of the Queensland Institute of Medical Research.

Family **TRICHOSTRONGYLIDAE**

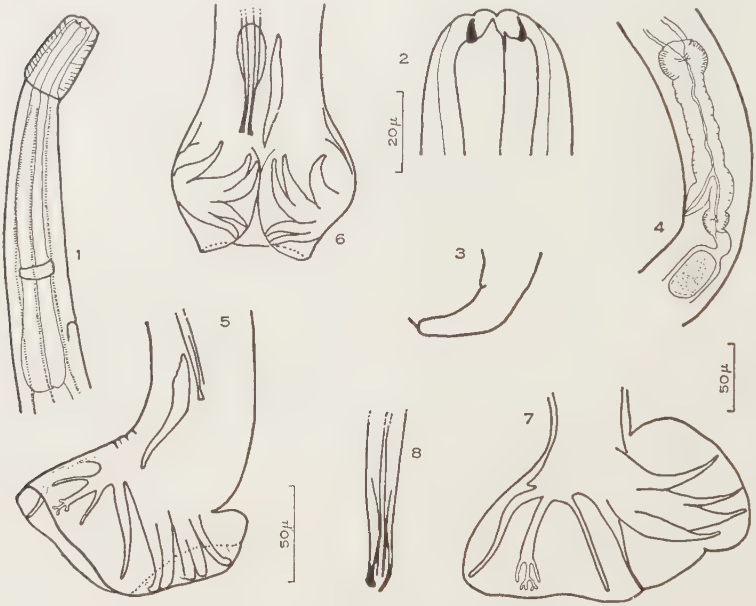
Trichostrongyles are apparently very common in bandicoots and five species are described below from the alimentary tract. Sometimes it has been difficult to assign the species to genera and the genera to subfamilies. The most recent comprehensive work on the group has been that of Skryabin, Shikhobalova, and Shults (1954) but their treatment of many genera has been somewhat arbitrary.

All five species from bandicoots have been assigned to separate genera, and of these three are proposed as new. Two species, *Nicollina iota*, sp.nov., and *Austrostrongylus acinocercus*, sp.nov., are placed in existing genera, with some reservation, as they do not show all the characters considered diagnostic in either genus. The main points of distinction between the two genera appear to be:

(1) Presence of a single dorsal tooth in *Nicollina* Baylis (cf. Baylis 1930*b*), and an accessory ventral tooth or teeth in *Austrostrongylus* Chandler (cf. Chandler 1924).

(2) The female tail ends bluntly and bears a spike in *Nicollina*, but is simple and conical, ending in a point in *Austrostrongylus*.

(3) The spicules end in 2 or 3 points in *Nicollina*, but in a single tip in *Austrostrongylus*.



Figs. 1–6.—*Nicollina iota* sp. nov.: 1, anterior end of male; 2, head; 3, tail of female; 4, region of vulva; 5, ventral view of bursa; 6, subdorsal view of bursa. Figs. 7 and 8.—*Nicollina* sp.: 7, subdorsal view of bursa; 8, tips of spicules. Figures 1, 3, 4, and 7 to same scale; Figures 5 and 6 to scale beside Figure 5; Figures 2 and 8 to scale beside Figure 2.

Neither of the two species under consideration shows all three of these characters of either genus. It seems quite unnecessary to erect two new genera, and the species have been allotted on the basis of spicule shape, this being less open to mistaken observation than the presence or absence of ventral teeth.

NICOLLINA IOTA, sp. nov.

Figs. 1–6

Hosts and localities.—I. obesulus, Dunorlan, Tas.; Cherry Gardens, S. Aust.; Innisfail, Qld.; Mt. Glorious, Qld. *P. nasuta*, Innisfail; Mt. Glorious.

Location.—Intestine.

Type host.—I. obesulus, Dunorlan, collected in June 1959 by J. Thompson.

This is a small species. When preserved in alcohol most of the specimens contract into more or less close spirals.

Cuticle of anterior end inflated and striated, both longitudinally and transversely, and raised into 2 lateral and 6 other longitudinal ridges, which are present, though narrow, throughout the body length. Buccal cavity very small and well cuticularized, with a large dorsal tooth and 2 ventral teeth. Oesophagus surrounded by nerve ring at about two-thirds of its length. Excretory pore at about three-quarters or more of the length of the oesophagus from the anterior end. Cervical papillae not seen.

Tail of female finger-like, ending bluntly in 2 shallow lateral lobes, between which projects a spine 15–20 μ long. Vulva, a transverse slit with no adjacent cuticular enlargement, lies near the posterior end. Posterior ovijector much shorter than the anterior (Fig. 4) and its muscular bulb smaller.

Bursa symmetrical and closely furled, its lobes hardly distinguishable from one another; arrangement of the rays shown in Figures 5 and 6. Spicules slender; each ends in 2 points, the longer of which is slightly enlarged, and the 2 longer tips are united by alae. Boat-shaped gubernaculum, 50–60 μ long.

The species differs from others of the genus in the presence of small ventral teeth, and the form of the dorsal ray, as well as being smaller.

The specimens from Queensland show the characters described above, but those concerned with the cuticle are more pronounced. In most of the Queensland specimens the inflated cervical cuticle is very strongly striated and is raised into bosses between successive striae. The longitudinal and transverse striae over the rest of the body are very distinctly developed, and the inside of the bursa is ridged, so much so that in many cases the details of the bursal rays, especially of the dorsal ray, cannot be seen. Measurements are given in Table 2.

In two male worms from *I. obesulus* from northern Queensland which are indistinguishable in other features, the spicule length is much less; other measurements of these two male worms have been listed separately in Table 2. Each of the aberrant specimens occurred in a host also infected with the typical form of the species.

NICOLLINA sp.

Figs. 7 and 8

One male worm from *I. obesulus* from Dunorlan differed from *N. iota* (present in the same host animal) in being longer, in having stouter spicules which were relatively shorter and with the tips unlike (Fig. 8), and in the shape of the bursa and arrangement of the rays (Fig. 7). The measurements are given in the right-hand column in Table 2.

AUSTROSTRONGYLUS ACINOCERCUS, sp. nov.

Figs. 9–13

Host.—*P. nasuta*, collected by D. G. Elliot.

Locality.—Innisfail, Qld.

Location.—Intestine.

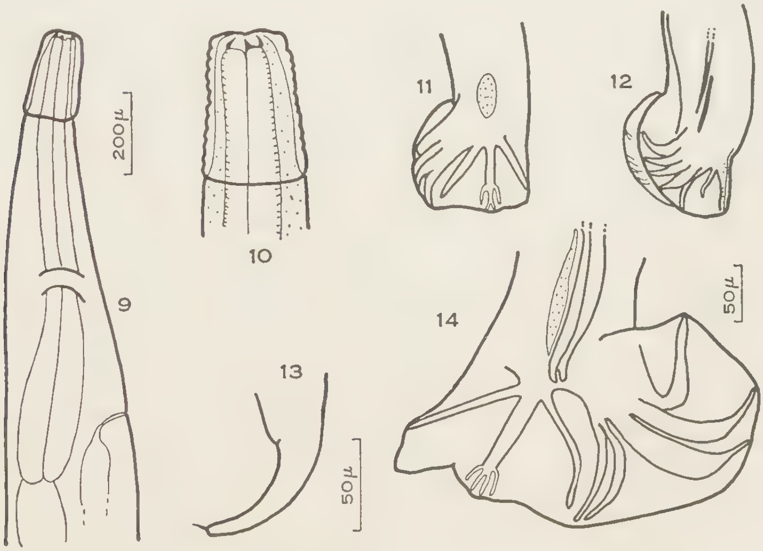
TABLE 2

MEASUREMENTS OF NICOLLINA SPECIES FROM VARIOUS LOCALITIES

Part Measured	*N. iota*							*Nicollina* sp.
	Tasmania			Queensland				Dunorlan, Tas.
	Range	Mean	No. of Specimens	Range	Mean	No. of Specimens	Two Aberrant Male Specimens	One Male Specimen
Male (mm)	2·2–2·9	2·5	10	2·0–3·3	2·1	14	2·3, 2·4	3·7
Oesophagus (μ)	220–350	297	7	240–290	260	13	250, 260	205
Cephalic cuticular inflation (μ)	55–60	62	6	42–60	50	10	53, 58	65
Anterior end to nerve ring (μ)	190–200	193	3	135–150	140	9	136, 135	150
Anterior end to excretory pore (μ)	228–240	235	3	185–220	194	10	225, 245	160
Spicule length (μ)	200–290	244	10	240–300	280	14	130, 130	200
Female (mm)	2·8–3·7	3·4	10	2·1–3·5	2·8	18		
Oesophagus (μ)	310–400	352	8	250–290	264	13		
Cephalic cuticular inflation (μ)	55–75	64	5	45–60	50	15		
Anterior end to nerve ring (μ)	—	200	3	135–150	144	9		
Anterior end to excretory pore (μ)	220–240	233	3	180–220	208	12		
Posterior end to vulva (μ)	390–500	471	9	300–600	428	17		
Tail (μ)	65–80	69	8	50–85	63	12		
Eggs (μ)	—	65 by 35	—	43–48 by 25–31	—	—		

Males 3·9–4·9 mm long, females 5·9–7·3 mm. Cephalic cuticle inflated and transversely striated, and, in two specimens, embossed; rest of the cuticle finely striated longitudinally. Longitudinal ridges not distinct. Buccal capsule with 1 dorsal tooth; ventral teeth, if present, very small.

Oesophagus club-shaped, 220–300 µ long in male and 250–280 µ in female. Nerve ring surrounds it shortly behind its mid-length, and excretory pore lies just in front of its posterior end. Female tail about 70 µ long, conical, and ending bluntly, bearing a short spine. Vulva an insignificant transverse slit, 1·0–1·1 mm from the posterior end. Uteri opposed; anterior ovijector very much longer than posterior. Eggs 35–40 µ by 20–22 µ.



Figs. 9–13.—*Austrostrongylus acinocercus*, sp. nov.: 9, anterior end of male; 10, head of female; 11, dorsal view of bursa; 12, lateral view of bursa; 13, tail of female. Fig. 14.—*Austrostrongylus* sp., bursa. Figures 10, 11, 12, and 13 to scale beside Figure 13.

Spicules 500–570 µ long, slender, and end in simple points. Gubernaculum about 30 µ long. Symmetrical bursa small, with ill-defined dorsal lobe and short lateral lobes. Arrangement of bursal rays shown in Figures 11 and 12.

The species is assigned to the genus *Austrostrongylus* on account of the spicule shape. The apparently single tooth and the shape of the tail distinguish it from other species of the genus.

AUSTROSTRONGYLUS sp.

Fig. 14

A single male worm from *I. obesulus* from Mt. Glorious, Qld., differs from other trichostrongyles collected. It is 8·1 mm long, with an annulated cephalic inflation 80 µ long. The rest of the cuticle is striated transversely and longitudinally, with 8 narrow longitudinal ridges, 2 of them lateral. The buccal capsule is well developed with 1 large dorsal and 2 smaller ventral teeth. The oesophagus, 480 μ long, is enlarged near the base. The nerve ring is 290 μ from the anterior end and the excretory pore was not observed. The spicules are 700 μ long, not divided at the distal ends, but slightly widened near the tip. The gubernaculum is 130 μ long. The bursa is wide and the arrangement of the rays is shown in Figure 14.

Genus PERAMELISTRONGYLUS, gen. nov.

Type species *P. skedastos*, sp. nov.

Generic diagnosis.—Cuticle with transverse and longitudinal striae, narrow lateral alae in the anterior region; no cephalic cuticular inflation; cervical papillae apparently absent; mouth surrounded by 6 distinct lips; buccal capsule and tooth absent. Female with transverse vulva near posterior end; tail without spine or accessory processes. Male with spicules elongate, alate, bifid; gubernaculum absent; prebursal papillae present; bursa longer dorsally than ventrally, ventral rays arise together from stem separate from lateral rays, externodorsal ray arises from nearly half length of doral ray; dorsal ray with 2 short lateral branches and 3 pairs of terminal branches. Parasitic in marsupials.

The absence of any cephalic inflation and of buccal capsule and tooth, and the presence of relatively long, simple spicules suggest that it belongs to a genus in the subfamily Graphidiinae Travassos (cf. Travassos 1937). It differs from *Graphidium* Railliet & Henry and *Graphidioides* Cameron in the absence of a gubernaculum and in the shape of the bursa, and from *Graphidiella* Cameron in the absence of prebursal papillae, absence of cervical papillae, mode of origin of the externodorsal ray, and in the structure of the ovijectors. In some features it resembles genera of Nochtiinae Skryabin & Shikhobalova, but differs in the absence of a cephalic inflation.

PERAMELISTRONGYLUS SKEDASTOS, sp. nov.

Figs. 15–27

Hosts.—*I. obesulus*, *P. nasuta*, and *P. gunni*.

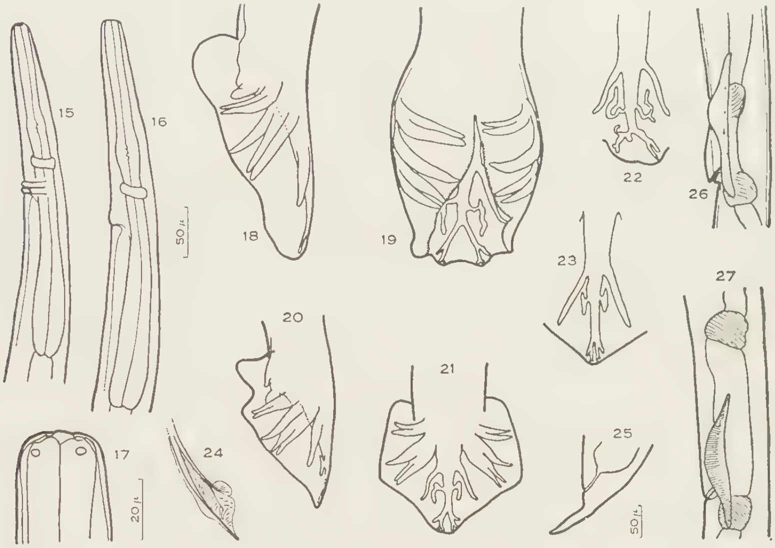
Localities.—North and south Queensland, Victoria, South Australia, Tasmania.

Location.—Most commonly in stomach. In one specimen also in ileum.

Type host.—*I. obesulus*, Innisfail, Qld., collected by Dr. M. J. Mackerras.

Cuticle striated transversely and longitudinally, transverse striae more distinct in both sexes at the extremities of the worms, and longitudinal striae more so over greater part of the body. Narrow lateral alae present in anterior third of body. Head simple, bearing 6 cephalic papillae; cephalic cuticular inflation absent. Buccal capsule and teeth are not developed. Oesophagus widens slightly towards its base. Excretory pore at about level of mid-oesophagus, and nerve ring shortly in front of this. Small circular excretory pore situated in a ventral groove between 2 prominent cuticular folds extending ventrally from side to side of the body. Cervical papillae not observed.

In female, body tapers suddenly near anus and the digitiform tail ends bluntly. Vulva, at one-sixth to one-seventh of body length from posterior end, a transverse slit on projection of body wall, and anterior lip swollen, overhanging posterior lip. At each side is a short cuticular ala. Anterior ovijector distinctly longer than posterior.



Figs. 15–27.—*Peramelistrongylus skedastos*, sp. nov.: 15, 16, anterior ends of forms A and B respectively; 17, head of form A; 18, 19, lateral, ventral views of bursa, form A; 20, 21, lateral and dorsal views of bursa, form B; 22, aberrant dorsal ray, form A; 23, dorsal ray, form C (from *Perameles gunni*); 24, tip of spicule; 25, tail of female, form A; 26, 27, region of vulva, forms A and B respectively. Figures 15, 23, 25, and 26 to scale beside Figure 25. Figures 16, 18, 19, 20, 21, 22, 24, and 27 to scale beside Figure 16.

Spicules long and slender, alate for most of their length, and each ends in 2 processes, supporting, and joined together by, fan-shaped expansions of alae. Bursa long dorsally, lateral edges curled inwards and hard to unfold. Arrangement of rays as shown in Figures 18 and 19. Shape of branches of dorsal ray, especially of proximal pair, subject to wide variation, an extreme example of which is shown in Figure 22.

There appear to be three variant forms of this species. One of these is found in some specimens from south Queensland (Mt. Glorious, Mt. Nebo), and is referred to below as form B. The second is found in nearly all the specimens from southern Australia and is referred to as form C. The typical form, A, comes from north Queensland and Brisbane, with one record from Mt. Glorious. The points of difference in forms A, B, and C are as follows:

(1) In forms B and C the position of the excretory pore is not marked by a ventral groove or roll of cuticle (Fig. 16).

TABLE 3

MEASUREMENTS OF THE VARIOUS FORMS OF PERAMELISTRONGYLUS SKEDASTOS

Part Measured	Form A: N. and S. Qld.			Form B: S. Qld.			Form C: Dunorlan, Tas.			Form C: S. Aust.*		Form C: Variants†	
	Range	Mean	No. of Specimens	Range	Mean	No. of Specimens	Range	Mean	No. of Specimens	Range	Mean	Range	Mean
Male													
Length (mm)	4·5–7·6	6·1	47	3·7–6·4	4·6	19	6·5–7·5	6·8	16	7·5, 8·2	7·8	6·8, 7·6	7·2
Oesophagus (μ)	425–510	473	15	330–460	427	16	540–620	604	15	500, 580	540	510, 570	540
Anterior end to excretory pore (μ)	220–260	242	10	170–240	207	13	250–290	267	12	234, 255	245	230, 270	250
Spicule (μ)	350–500	445	22	310–420	356	16	510–640	613	15	550, 610	580	550, 520	535
Female													
Length (mm)	5·2–9·1	7·4	46	4·6–8·0	6·0	17	6·5–9·2	8·4	16	9, 11	10	6·5, 7·5	7·0
Posterior end to vulva (mm)	0·7–1·5	1·1	31	0·7–1·2	0·9	14	1·0–1·5	1·3	16	2·1, 2·1	2·1	1·3, 1·6	1·45
Oesophagus (μ)	420–550	504	10	370–510	389	13	550–650	598	16	600, 680	640	550, 510	530
Anterior end to excretory pore (μ)	230–270	250	9	190–260	220	13	250–290	273	12	240, 270	255	240, 260	250
Tail (μ)	90–120	100	10	65–100	82	13	70–80	78	3	95, 99	97	90, 100	95
Eggs (μ)	50–63 by 30–40	—	—	50–55 by 30–40	—	—	70 by 40	—	—	60–70 by 40	—	65 by 37–39	—

* Specimens from Cherry Gardens.

† Two males and first female specimen from Ararat, Vic., other female from Cherry Gardens.

(2) In forms B and C the point of origin of the 2 main branches of the dorsal ray is a little nearer the bursal edge and the lateral branches given off from them originate nearer this bifurcation. This is rather more marked in form C (Fig. 23) than in form B (Fig. 21), and in both these the distal part of the dorsal ray is thicker than in form A (Fig. 19).

(3) There is no marked enlargement of the ventral part of the body near the vulva in either form B or form C.

(4) In form B the alae at each side of the vulva extend from the level of the posterior ovijector sphincter through about half the distance from vulva to anterior sphincter (Fig. 27). In form A (Fig. 26) and form C these alae extend to, or past, the anterior sphincter. The difference is partly due to the comparatively greater length, in form B, of the whole anterior ovijector. In form B these alae are strongly cross-striated, while in forms A and C striations, if present, are very faint.

However, in the only female among the specimens from Victoria, and in one of the three females from South Australia, the vulvar alae are short. Measurements of these specimens are given in the last column of Table 3.

These differences are small and only of degree, and are not considered sufficient to distinguish separate species. They are, however, constant and are linked, at least in part, with variation in the habitat of the host, and they possibly indicate the beginning of speciation. In no case did one host animal harbour more than one of the three forms. Before any pronouncement is made as to the status of the variant forms, it will be necessary to examine many more specimens, especially from southern Australia and from New South Wales.

Distribution.—The localities and host animals from which the various forms of *P. skedastos* have been recorded are set out in Table 4. *P. skedastos* has also been identified from the water rat, *Hydromys chrysogaster*, and the pouched mouse, *Phascogale flavipes* (Waterhouse). Both collections were from Innisfail, and all specimens were form A.

Genus MACKERRASTRONGYLUS, gen. nov.

Type species *M. peramelis* (Johnston & Mawson).

Generic diagnosis.—Cephalic cuticular inflation present; cuticle with transverse and longitudinal striae, narrow lateral alae, and 4 narrow submedian longitudinal ridges; mouth surrounded by 6 small lips; no tooth; buccal capsule insignificant. *Female*: tail ending in 2 small processes and a spine; transverse vulva with overhanging anterior lip near posterior end of body; 2 uteri and ovaries. *Male*: with short trifid spicule; gubernaculum present; small prebursal papillae present; lateral and ventral rays from same base; ventrals directed ventrally; externodorsal ray from base of dorsal; dorsal ray stout and long, giving off a pair of lateral branches ending in bifid tips. Parasites of marsupials.

In view of the inflated cervical cuticle, relatively short complex spicules, and complex female tail, *Mackerrastrongylus* belongs in the subfamily Anoplostrongylinae. It most closely resembles *Fontesia* Travassos and *Pholidostrongylus* Baer, differing from them chiefly in the form of the spicules.

Mackerrastrongylus peramelis (Johnston & Mawson)

Figs. 28–31

Filarinema peramelis Johnston and Mawson, 1938, pp. 196–7.

Type host and locality.—*I. obesulus*, south Queensland.

New records.—*I. obesulus*, Innisfail, Miriwinni, Mt. Glorious, Brisbane. *P. nasuta*, Innisfail, Mt. Glorious.

A large number of specimens is now available of the species originally described as *Filarinema peramelis*. It appears to be a very common parasite in Queensland, but has not been recorded from other States.

Table 4

DISTRIBUTION OF THE VARIOUS FORMS OF PERAMELISTRONGYLUS SKEDASTOS IN BANDICOOTS

Host	Locality	No. of Host Animals in which *P. skedastos* Found			
		Form A	Form B	Form C	
I. obesulus	Innisfail, Qld.	9			
	Miriwinni, Qld.	2			
	Babindi, Qld.	1			
	Whyanbeel, Qld.	1			
	Mossman, Qld.	2			
	Mt. Glorious, Qld.	1	5		
	Mt. Nebo, Qld.		1		
	D'Aguillar, Qld.	1			
	Brisbane	8			
	Dunorlan, Tas.			2	
	Ararat, Vic.				1*
	Cherry Gardens, S. Aust.			1	1*
P. nasuta	Mt. Glorious		1		
P. gunni	Dunorlan			1	

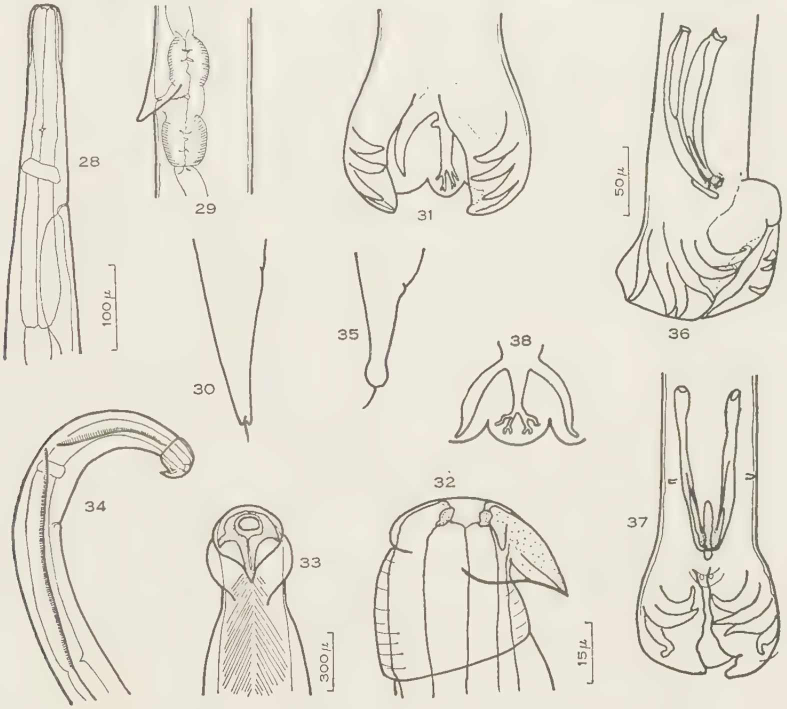
* Variants of form C.

Ten worms of each sex from each host species both from north and south Queensland have been measured and the results are given in Table 5. The type material has been re-examined and the new material compared with it. Additional information on the morphology is that the cuticle is raised into 6 narrow longitudinal crests. No indication can be seen of any special structure at the anterior end of the oesophagus, as described by Mönnig (1929, p. 307) for the type species of *Filarinema*. Largely because of this special feature (which was, however, not included by Mönnig in his generic diagnosis) a subfamily, Filarineminae Skryabin & Shikhobalova, was erected for *Filarinema*. On the basis of other characters, *Filarinema* is very close to *Asymmetricostrongylus* Nagaty.

Genus ASYMMETRACANTHA, gen. nov.

Type species *A. tasmaniensis*, sp. nov.

Generic diagnosis.—Body elongate, widest posteriorly; cervical and lateral alae present; head bent ventrally, with asymmetrical cephalic inflation extended ventrally and partly cuticularized to form a large ventral hook, the base of which is connected with an imperfectly chitinized buccal ring. Tail of female ending in a swollen tip bearing a spine. Vulva about one-fifth to one-sixth of body length from the tail. Spicules short, bifid; gubernaculum present; prebursal papillae present. Bursa with dorsal lobe; ventral and lateral rays arising from same base, ventrals directed ventrad, medio- and externolaterals directed dorsad; externodorsal arising from base of dorsal ray; dorsal ray bifurcating at distal quarter, each half ending in 3 branches. Parasitic in marsupials.



Figs. 28–31.—*Mackerrastrongylus peramelis*, sp. nov.: 28, anterior end; 29, region of vulva; 30, tail of female; 31, bursa, ventral view. Figs. 32–38.—*Asymmetracantha tasmaniensis*, sp. nov.: 32, head, lateral view; 33, head, ventral view; 34, oesophageal region; 35, tail of female; 36, 37, lateral and ventral views of bursa; 38, externodorsal and dorsal rays. Figures 28, 29, and 34, to scale beside Figure 28. Figures 30, 31, 35, 36, 37, and 38 to scale beside Figure 36.

The nearest affinities of *Asymmetracantha* appear to be with the subfamily Anoplostrongylinae, although all the genera of this group have a complex female tail, ending in 2 or more small cones as well as a terminal spine. There are also close resemblances to *Molineus* spp., and according to the key given by Skryabin,

TABLE 5

MEASUREMENTS OF MACKERRASTRONGYLUS PERAMELIS FROM TWO HOSTS FROM VARIOUS LOCALITIES

Each average is for 10 specimens unless otherwise indicated in parenthesis

Part Measured	From North Queensland				From South Queensland				Type Material
	I. obesulus		*P. nasuta*		*I. obesulus*		*P. nasuta*		
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	
Male									
Length (mm)	6·2–7·5	6·8	5·7–6·7	6·1	4·4–5·2	4·7	4·0–4·4	4·2 (4)	4·6–4·9
Oesophagus (μ)	410–480	442 (6)	380–420	397 (9)	330–380	350	310–350	332 (4)	350–380
Anterior end to excretory pore (μ)	250–290	270	260–290	272 (9)	200–240	220	200–230	210 (4)	220
Spicule (μ)	230–250	242	210–240	226	140–170	153	120–150	138 (4)	140–150
Gubernaculum (μ)	58–80	66 (3)	60–80	72 (7)	70–80	77 (5)	60–75	68 (4)	
Cephalic cuticular inflation (μ)	80–90	84 (4)	80–90	85 (5)	65–70	66 (3)	59–83	69 (4)	
Female									
Length (mm)	8·0–11·2	10·1	7·3–9·6	8·5	5·7–7·0	6·3	5·8–6·8	6·3	5·8–6·0
Oesophagus (μ)	470–520	502	430–470	448	350–440	407	370–410	390	
Anterior end to excretory pore (μ)	280–300	291 (8)	250–300	274	180–250	224 (9)	230–270	249	
Tail (μ)	110–130	120 (9)	80–130	111	70–110	92	80–110	102	80–90
Posterior end to vulva (mm)	2·1–2·9	2·4	1·7–2·3	1·9	1·2–1·4	1·3 (7)	1·3–1·5	1·4	1·1
Eggs (μ)	55–60 by 36–40	—	47–53 by 27–30	—	50 by 30	—	53–60 by 27–36	—	—

Shikobalova, and Shults (1954, p. 39) *Asymmetracantha* belongs in the subfamily Molineinae Skryabin & Shults.

Asymmetracantha differs from the other two genera in which ventral cephalic hooks are present in the mode of origin of the hooks. In *Strongylacantha* Beneden (cf. Beneden 1873) they project directly from the buccal capsule and are not associated with the cuticle on the outer surface of the head. In *Biacantha* Wolfgang they are formed from thickenings of the inflated cephalic cuticle. In *Asymmetracantha* they appear to be formed as in *Biacantha* but have some basal connection with the small and imperfectly developed buccal ring. *Asymmetracantha* also differs from *Biacantha* in the presence of cervical and lateral alae and in the shape of the female tail.

ASYMMETRACANTHA TASMANIENSIS, sp. nov.

Figs. 32–38

Hosts and localities.—*I. obesulus*, Dunorlan, Tas.; *P. nasuta*, Mt. Glorious, Qld.

Location.—Small intestine.

Type host.—*I. obesulus*, collected in June 1959 by J. Thompson.

Long and slender species, tapering anteriorly, especially the female, in which the posterior half is about twice the diameter of the anterior. The single specimen (a male) from *P. nasuta* is smaller but otherwise similar.

Anterior end of body bent ventrally; cuticle inflated, thickened at anterior end, and forming 1 large ventral and 2 small subventral teeth which project outwards, very much as described for *Biacantha demodex* (Wolfgang 1954). Base of large tooth has some connection with slightly thickened cuticle around mouth opening, which forms a shallow, imperfectly chitinized buccal ring. There are 6 papillae around mouth opening. Behind cephalic inflation lateral cervical alae reach level of nerve ring, and behind these lateral alae arise on dorsal surface and swing round to lateral positions; these extend nearly as far as the bursa in the male, and to the vulva in the female. Alae transversely striated and rest of body behind cephalic inflation bears obliquely longitudinal striae sloping from the mid-dorsal and mid-ventral line to lateral lines. Male has also a pair of subventral longitudinal ridges or alae, also transversely striated.

Oesophagus only slightly wider towards base. Nerve ring just in front of, and excretory pore just behind, mid-oesophagus. Vulva a transverse slit near posterior end of body; eggs thin-shelled. Posterior end of female tapers rapidly just in front of anus, and short tail ends in spherical knob bearing fine cuticular spine.

Prebursal papillae are present in male. Bursa with small dorsal lobe, arrangement of bursal rays as shown in Figures 36, 37, and 38. Spicules equal, each ending in 2 branches, of which longer outer one bears a short barb at right angles to shaft. The 2 tips of both spicules appear united by a less strongly cuticularized part of the spicule, which looks like a spongy ball between tips of each spicule, indicated in Figures 36 and 37 by dots. Gubernaculum present.

Measurements of male and female specimens taken from *I. obesulus* and of the single male specimen from *P. nasuta* are set out in Table 6.

Genus LABIOBULURA Skryabin & Shikhobalova

Subulura Molin, 1860 (pro parte). Skryabin and Shikhobalova, 1948, pp. 189–91.

The variations in the structure of the head, buccal cavity, and associated structures in the Subuluridae has been described by Inglis (1958) and further work from him is pending. Inglis accepts the genus *Labiobulura* Skryabin & Shikhobalova which was erected for *Subulura peramelis* Baylis, and includes *S. peragale* Johnston & Mawson, with the proviso that this species was erroneously described with 6 lips instead of 12. The present author has re-examined the paratype specimens of *S. peragale* and now re-affirms the presence of only 6 lips. A short redescription of the species is included below. *Labiobulura* spp. have been described only from bandicoots.

Table 6

MEASUREMENTS OF MALE AND FEMALE SPECIMENS OF ASYMMETRACANTHA TASMANIENSIS FROM HOST ANIMALS I. OBESULUS AND P. NASUTA

Ranges given are for 8 males and 9 females

Part Measured	*I. obesulus*		*P. nasuta*
	Males	Females	Male
Length (mm)	3·5–4·0	3·6–4·6	2·9
Max. diameter (μ)	70–83	110–140	—
Oesophagus (μ)	360–400	390–470	330
Spicule length (μ)	120–130		115
Gubernaculum (μ)	55–60		60
Tail length of female, excluding spike (μ)		75–90	
Tail spike (μ)		18–20	
Eggs (μ)		55–60 by 38–42	
Distance of vulva from posterior end (μ)		650–900	

Labiobulura peramelis was described by Baylis from *I. obesulus* from north Queensland. Johnston and Mawson have recorded it three times:

(1) Two female worms from *P. nasuta* from New South Wales (Johnston and Mawson 1939*a*, p. 204), with a note that the lips are longer and the buccal capsule larger than in the type specimens.

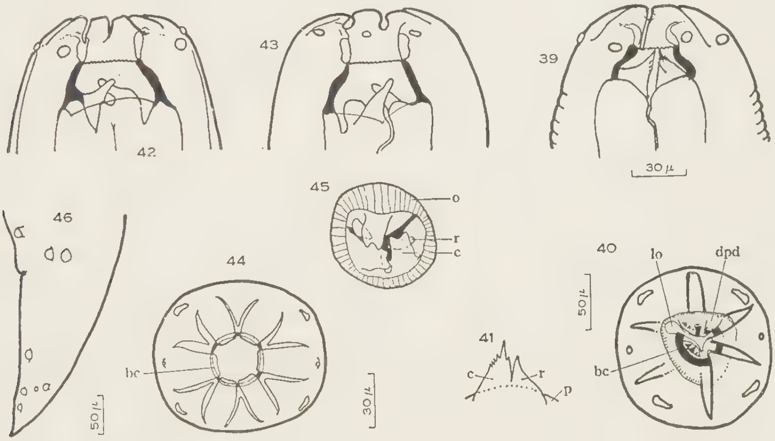
(2) From *P. bouganvillei* (syn. *P. myosura*) from Western Australia (Johnston and Mawson 1939*b*, p. 309) with a similar note.

(3) From *I. obesulus* (syn. *I. torosus*) from southern Queensland (Johnston and Mawson 1951, p. 36). These specimens were in poor condition.

In the course of the present study all of this material has been re-examined, as well as a number of other collections from bandicoots from south Queensland, South Australia, and Tasmania.

All the *Labiobulura* specimens found in these collections are very similar in build, size, and details of the male tail, but three species have been distinguished on the characters of the lips and buccal cavity. Externally the difference lies in the length of the cuticular grooves separating the lips, and in the shape of the anterior end. In the buccal cavity the differences lie mainly in the shape of the oesophageal derivatives lying in the base of the buccal cavity.

It was debated whether these differences are of specific or varietal value. As they are apparently at least partly linked with a difference in geographical distribution, and as they are morphological rather than mensural, and, moreover, as the characters of the head are those chiefly concerned in specific and generic differentiation in the Subuluridae as a whole, the three forms are regarded as distinct species.



Figs. 39–41.—*Labiobulura peragale* (Johnston & Mawson): 39, head in ventral view; 40, *en face* view of head, with 4 lips and part of buccal capsule not drawn, to show underlying pharyngeal derivative; 41, chordal lobe, radial lobe, and part of one peripheral lobe as seen from inside mouth. Figs. 42–46.—*Labiobulura peramelis* (Baylis): 42, 43, and 44, dorsal, lateral, and *en face* views of head; 45, optical section of anterior end of oesophagus, showing pharyngeal derivative; 46, tail of male. Figures 41, 42, 43, 44, and 45 to scale beside Figure 44. *bc*, Buccal capsule, the dorsal part of which is not drawn; *c*, chordal lobe; *dpd*, dorsal pharyngeal derivative; *lo*, lumen of oesophagus; *o*, oesophagus; *r*, radial lobe.

In a private communication Mr. Inglis has stressed the importance of comparing dorsal views of different species. From the present study it seems that longitudinal sections through the head, as well as views from all aspects including *en face*, are necessary before the structure of the pharyngeal derivative is ascertained.

In view of the redescriptions given below, a slight modification must be made in the generic diagnosis given by Inglis (1958, p. 595) in regard to the number of lips (if *L. peragale* be retained in the genus), and the presence of cervical alae. (The use of the term "cephalic alae" in this diagnosis and that of *Aulonocephalus* and *Allodapa* is presumably an error.) Cervical alae are present in all specimens examined. Those of *L. peragale* are, as stated in the original description, narrow, but quite distinct.

TABLE 7

MEASUREMENTS OF LABIOBULURA SPECIES FROM VARIOUS LOCALITIES

Part Measured	*L. peramelis*			*L. baylisi*		*L. inglisi*			
	Queensland*	Queensland		Queensland		Cherry Gardens, S. Aust.	Nuyts I., S. Aust.	Dunorlan, Tas.	Western Australia
Male									
Length (mm)	7·9–9·2	7·0–9·9	10·9	11·7–12·3	13·5	9·8–11·8	6·4–7·7	11·7–15·2	
Max. breadth (μ)	300–330	—	327	310–350	—	400	250–330	440	
Oesophagus (mm)	1·5	1·5–1·9	1·7	1·6–1·7	1·6	1·4–1·5	1·1–1·3	1·6–1·9	
Anterior end to nerve ring (μ)	—	—	420	410–450	410	—	230–330	400–500	
Anterior end to excretory pore (μ)	—	—	600	600–680	570	—	350	600–700	
Spicule (mm)	2·0–2·2	1·8–2·3	2·9	2·2–2·5	2·1	2·0–2·4	1·5–1·9	2·3–2·6	
Gubernaculum (μ)	150–170	130–150	172	150	156	150–160	—	160–170	
Tail (μ)	200	160–180	200	200–210	250	170–200	130–160	200–270	
Female									
Length (mm)	11·0–12·7	15·8–19·8	20·3	16·5–18·0	21	5·8–19·3	8·1–10·8	14·0–23·0	11·1
Max. breadth (μ)	350–400	450	450	450–500	—	380–450	340	570	450
Oesophagus (mm)	1·5–1·8	1·7–1·9	2·2	2·0–2·2	1·9	1·74	1·2–1·5	1·5–2·3	1·7
Anterior end to nerve ring (μ)	—	—	550	450	—	—	—	—	—
Anterior end to excretory pore (μ)	—	—	750	640–750	650	—	—	—	—
Anterior end to vulva (mm)	4·5–5·2	4·5–5·9	7·9	6·3–7·1	9·0	5·8–7·8	3·3–3·5	—	7·5
As % of length	41	35–40	38	38–40	41	36–41	30–40	30–38	48
Tail (μ)	400–560	610–700	800	650–800	900	—	—	900–1250	?900
Eggs (μ)	67·5–87·5	65–75 by 45–55	—	61–65 by 47–53	—	55–70 by 40–47	70–75 by 50–55	—	—

* Measurements of Baylis (1932).

LABIOBULURA PERAGALE (Johnston & Mawson)

Figs. 39–41

Subulura peragale Johnston and Mawson, 1940, pp. 472–3.

The paratype material of this species, from *Thalacomys minor* ("*Peragale minor*"), has been re-examined, and an *en face* view drawn of the head. There are only 6 lips. The buccal capsule is circular in section. In the pharyngeal portion the radial lobes are distinctly shorter than the chordal lobes and form a blunt anterior projection. Each chordal lobe is wide at the base, and ends distally in about 3 or 4 short spines grouped around the base of 1 long spine. The short spines are most clearly seen in longitudinal section of the head, but could also be distinguished in *en face* view. In ordinary whole mount they do not show through the other structures. This difference in configuration of the chordal lobes, linked with the smaller number of lip lobes, may indicate a distinct genus, but it is not thought proper to introduce this while the whole family Subuluridae is being revised by Mr. Inglis.

LABIOBULURA PERAMELIS (Baylis)

Figs. 42–46

Subulura peramelis Baylis, 1930*a*, pp. 354–66.

This species is now recorded from *I. obesulus* from Yandina and Bardon, both in south Queensland. Many of the specimens are larger than those recorded by Baylis and the eggs are smaller, and rather oval than subglobular in shape. Lateral alae are present in both sexes in the oesophageal region. In the better preserved males an additional pair of small papillae is clearly seen near the tip of the tail (Fig. 46). These may be phasmids.

Most of the measurements given in Table 7 are from eight females and six males, except those of the nerve ring, oesophageal bulb, and phasmid, which were taken from two females 18·5 and 20·3 mm long, and one male 10·9 mm long. It is not stated by Baylis whether his measurements of the nerve ring and head are from male or female specimens.

The specimens previously recorded as belonging to this species from *P. nasuta* (Johnston and Mawson 1939*a*, p. 204) and from *I. obesulus* (*I. torosus*) (Johnston and Mawson 1951, p. 36) prove on re-examination to belong not to this species but to *L. baylisi*, sp. nov.

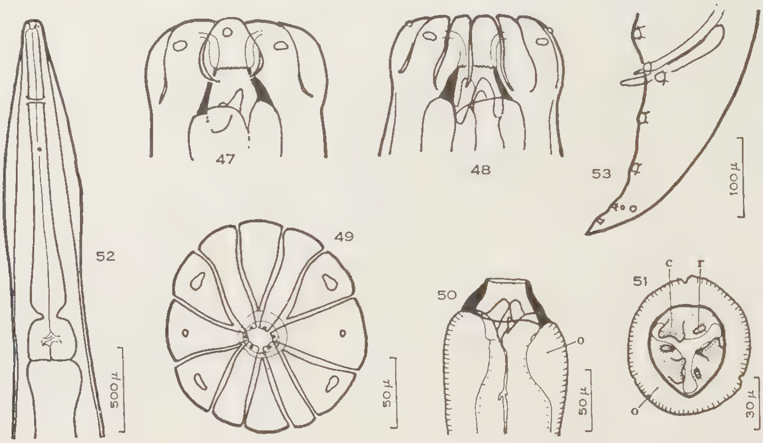
LABIOBULURA BAYLISI sp. nov.

Figs. 47–53

Type host and locality.—*I. obesulus*, Mt. Nebo, Qld., February 1958. Other localities for the same host are Mt. Glorious and Bardine, Qld.

This species is proposed for a large number of specimens which closely resemble *L. peramelis* in all but the morphology of the anterior end. Two female worms from *P. nasuta* from New South Wales, which were previously assigned to *Subulura peramelis* by Johnston and Mawson (1939*a*, p. 204) have been re-examined and found to belong to this species.

Head constricted below level of lips, whereas that of *L. peramelis* tapers to a rounded end. Lips more deeply incised. Papillae lie nearer to free ends of lips and not, as in *L. peramelis*, at or behind bases of lips. This last character, as well as nuchal constriction, is independent of whether lips are open or closed over mouth, and is not apparently associated with age or size. Wide cervical alae present in the oesophageal region. Shape of the radial and chordal lobes not differing very much from that of *L. peramelis*, but radial lobes not twisted to the same extent. Shape of male tail and arrangement of caudal papillae very similar in the two species.



Figs. 47–53.—*Labiobulura baylisi*, sp. nov.: 47, 48, 49, lateral, dorsal, and *en face* views of head; 50, ventral view of anterior end of oesophagus; 51, *en face* view of anterior end of oesophagus, looking onto pharyngeal derivative; 52, anterior end of body; 53, tail of male. Figures 47, 48, and 50 to scale beside Figure 50. *c*, Chordal lobe; *o*, oesophagus; *r*, radial lobe.

The measurements given in Table 7 are of 10 males and 10 females from *I. obesulus* from Mt. Nebo, and are typical of most of the specimens. Those of a particularly long male and female are given in the adjoining column.

LABIOBULURA INGLISI, sp. nov.

Figs. 54–59

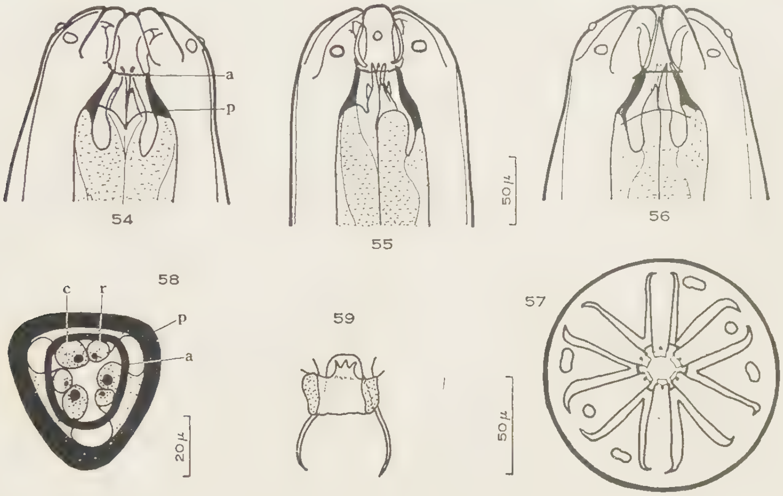
Hosts and localities.—*I. obesulus*, Dunorlan, Tas., Cherry Gardens, S. Aust.; *I. nauticus*, Nuyt's I., S. Aust.; *P. gunni*, Dunorlan.

Type host.—*I. obesulus*, Cherry Gardens, collected in September 1958 by A. Kowanko.

Only one female can be found of the material from *P. bougainvillei*, from Western Australia, recorded as *Subulura peramelis* Baylis by Johnston and Mawson (1939*b*, p. 309). This is not a good specimen, but the form of the lips and what can be seen of the internal mouth structures, indicate that it belongs to *L. inglisi*.

The specimens from the different localities vary in length, but not in proportions. Their measurements are given separately in Table 7.

General appearance very similar to that of *L. peramelis*: head tapers in the same way, cuticle is transversely striated, and cervical alae are present. Mouth surrounded by 12 lips, but these are separated from one another by long grooves which, though longer than in *L. peramelis*, are shorter than in *L. baylisi*.



Figs. 54–59.—*Labiobulura inglisi*, sp. nov.: 54, 55, 56, and 57, ventral, lateral, dorsal, and *en face* views of head; 58, looking into buccal cavity after lips, buccal capsule, and body wall removed; 59, part of buccal capsule and one lip, internal view. Figures 54, 55, and 56 to scale beside Figure 56. *a* and *p* (Fig. 54) indicate the level of rings *a* and *p* in Figure 58, i.e. the anterior and posterior ends of the peripheral lobe.

Structure of walls of buccal cavity and of oesophageal derivatives on same plan as those of other *Labiobulura* species, but whole structure relatively longer, and radial and chordal lobes very different in shape from those of other species (Figs. 54–56); rod-like parts of chordal lobes chitinized and apparently rigid; radial lobes less strongly chitinized, except at extremities.

The "forward prolongations of the buccal cavity lining" referred to by Inglis for *Labiobulura* species are distinctly seen in this species—they are not "smoothly rounded" but each ends in 3 small lobes (Fig. 59).

Measurements are given in Table 7 and details of the head and male tail are shown in Figures 54–59.

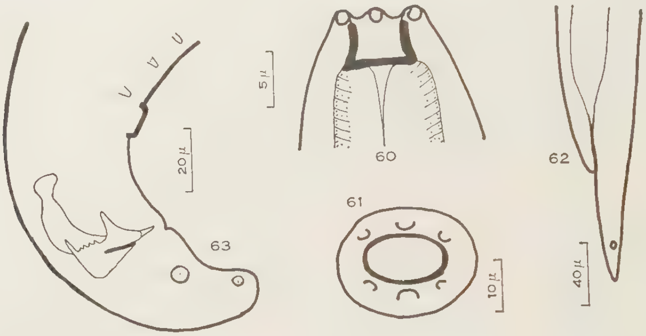
PARASTRONGYLOIDES AUSTRALIS, sp. nov.

Figs. 60–63

Hosts and localities.—*I. obesulus*, Cherry Gardens, S. Aust.; Ararat, Vic.; Dunorlan, Tas. *P. gunni*, Dunorlan.

Type host.—*I. obesulus*, Cherry Gardens, collected in September 1958 by A. Kowanko.

All of the southern Australian bandicoots which were examined while fresh were found to be infected with an apparently new species of *Parastrongyloides*. Mackerras (1959) has described *P. peramelis* and a related species, *Strongyloides thylacis*, which she found commonly, together or separately, in Queensland bandicoots. Dr. Mackerras has very kindly given me some of her named material. The specimens now recorded differ from *P. peramelis* in being larger, in the papillation of the male tail and its shape, and in the size of the eggs. They are, however, similar in other respects.



Figs. 60–63.—*Parastrongyloides australis*, sp. nov.: 60, anterior end; 61, *en face* view of head; 62, tail of female; 63, tail of male.

Males 1·6–2·3 mm long, 50–60 μ max. diameter; females 2·8–3·1 mm long, 60–80 μ max. diameter. Cuticle finely striated both longitudinally and transversely, and fine but distinct lateral alae present along almost whole length of body. Body thicker posteriorly in both sexes, and curved, not coiled, at posterior end in male. In Tasmanian specimens whole body coiled in about 3 turns in both sexes. Head bears 6 lip-like lobes each with a papilla. Buccal capsule oval in section, 5 μ long and 7 μ wide in male, a little larger in female. Oesophagus 500–700 μ long in male, 750–850 μ in female; anterior third is narrower than rest. Nerve ring and excretory pore just anterior to widening of oesophagus, 190–210 μ and 160 μ respectively from anterior end in female.

Vulva 1·1–1·2 mm from posterior end. Eggs 45–50 μ by 25 μ. Female tail 70–75 μ long, conical with blunt tip.

Male tail 30–45 μ long and *c.* 30–45 μ wide at anus, rounded posteriorly, without a terminal spine, such as occurs in *P. peramelis*: two pairs of caudal papillae present (Fig. 63). About a tail length in front of anus is a median papilla, and in front of this on each side is a longitudinal row of *c.* 10 small papillae. Spicule 35–40 μ long, measured directly from tip to tip, its shape similar to that of *P. peramelis*. Gubernaculum appears to be formed of 2 lateral wings with indented anterior margins curving around the spicules, and uniting to form a posterior keel. Structure of male tail in most particulars strikingly like that seen in marine, free-living nematodes belonging to the genus *Thoracostoma* Marion.

TRICHURIS PERAMELIS Baylis

Trichuris peramelis Baylis, 1932, pp. 31–2.

Host and locality.—I. obesulus, Dunorlan, Tas.

Location.—In lower small intestine, caecum, and rectum.

The Tasmanian specimens are larger than those described by Baylis (1932) and show some small differences.

Posterior part of body very much wider than anterior and in most specimens dark brown in colour. A single male specimen had the following dimensions: length 18·4 mm, oesophagus 11·4 mm (ratio of body length to oesophageal length 1 : 1·6), maximum width 350 μ, that at base of oesophagus 60 μ and near head 6 μ. Spicule length 1·4 mm, its sheath spinose except at distal end which is expanded into a bulb as described by Baylis, but more regular in outline.

Females 14–20 mm long, and ratio of oesophageal region to body length varies from 1 : 1·4–1·5. Maximum breadth 350–500 μ, that at vulva 150–200 μ, and at head about 15 μ. Anus situated just ventral to posterior end on a small papilla-like structure. Eggs smooth-shelled, 65 μ by 30–35 μ.

The main points in which these specimens differ from Baylis's description are in the shorter spicules, larger eggs, and in the presence of a bacillary band, occupying about one-quarter of the body circumference and extending from the head nearly to the base of the oesophagus. This band is not mentioned by Baylis; however, as the author has examined a male worm from *I. obesulus* from Queensland (length 16 mm, spicule 2 mm) in which such a bacillary band is also present, this is not considered to indicate a different species.

CAPILLARIA sp.

Hosts and localities.—I. obesulus, Dunorlan, Tas.; *P. gunni*, Dunorlan.

No males were present in this material, although there were numerous females with ripe eggs. The females are 15·5–20·0 mm long; the anterior and posterior parts of the body are in the ratio of 1 : 2. The cuticle is marked with fine longitudinal and transverse striae, and 2 indistinct bacillary bands, each about one-third of the body diameter, are present. The vulva is at the level of the base of the oesophagus, and in most specimens is not salient. The eggs are about 47 by 25 μ, with large polar plugs, and chased shells.

No *Capillaria* sp. has been described from Australian marsupials, although there are records of a collection from the oesophagus of *I. obesulus* in Queensland (Mackerras, Mackerras, and Sandars 1953).

ACKNOWLEDGMENTS

I am greatly indebted to Dr. M. J. Mackerras, Queensland Institute of Medical Research, for the loan of all the Queensland material, as well as to those who made the collections, namely Miss M. L. Emanuel, Miss D. G. Elliot, and Dr. Mackerras herself. The bandicoots from Tasmania were obtained by Mr. J. Thomson, Zoology Department, University of Melbourne, that from Victoria by Miss Phyllis Pilton, and from South Australia by Mr. A. Kowanko, both of the Zoology Department, University of Adelaide. I am also indebted to Mr. G. B. Sharman, whose wide connections with other mammologists made possible the collection of fresh material; and to Mr. J. H. Calaby, Wildlife Survey Section, C.S.I.R.O., for advice on the naming of *I. obesulus*.

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A REVIEW OF THE GENUS *LETHOCERUS* (HEMIPTERA: BELOSTOMATIDAE) IN THE EASTERN HEMISPHERE WITH THE DESCRIPTION OF A NEW SPECIES FROM AUSTRALIA

By A. S. Menke*

[*Manuscript received June 25, 1959*]

Summary

A new species of *Lethocerus* Mayr is described from Australia. *L. insulanus* (Montandon) is reported from Australia for the first time, making two the number of species known to occur in that country. *L. indicus* (Le Peletier & Serville) is tentatively listed as occurring in Australia and *L. edentulus* (Montandon) is synonymized with *L. insulanus*. A key to the eastern hemisphere *Lethocerus* is given and is supplemented with a synonymical list including all known names pertaining to the genus in the eastern hemisphere. *Kirkaldyia* Montandon is synonymized with *Lethocerus*.

Introduction

Through the courtesy of Dr. T. E. Woodward, University of Queensland, I have been able to examine a large series of *Lethocerus* Mayr from Australia and have found an undescribed species. Two species have been reported from that country, *L. indicus* (Le Peletier & Serville) and *L. edentulus* (Montandon). I have not seen *indicus* from Australia and suspect that *insulanus*, previously not recorded from that country, has been confused with that species by earlier workers, although it is possible that *indicus* may occur in the north-eastern part of the continent. *L. insulanus* and the new species described here are the only species known to me from Australia. *L. edentulus* was described from a single specimen collected at Rockhampton, Qld.; and, according to Montandon (1898),† was deposited in the Hamburg Museum, Germany. Dr. H. Weidner of that institution has informed me that the specimen cannot be found and is presumed lost during the war. The only character mentioned by Montandon in his very brief description was that the inner apical angle of the hind tibia was truncate. He stated that in all other respects the specimen looked like *insulanus*. All Australian *Lethocerus* and, in fact, all eastern hemisphere species that I have examined have very conspicuous projections at the inner apical angle of the hind tibia, and this suggests that Montandon may have had a specimen of *insulanus* in which the projection had been broken off or ill-formed. I feel, therefore, that *edentulus* should be reduced to a synonym of *insulanus*.

Lethocerus distinctifemur, sp. nov.

Size.—Length 55–69 mm; width 20·5–25 mm.

Description.—Ratio of eye width to greatest interocular distance 3·5 : 3; ratio of greatest interocular distance to least interocular distance 3 : 2; lateral margins of pronotum nearly straight; anterior lobe of pronotum with 2 poorly

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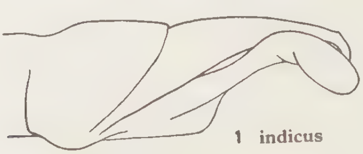
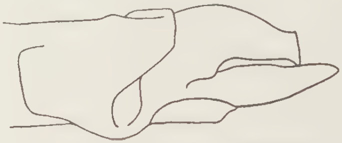
* University of California, Davis, California.

† Montandon, A. L. (1898).—Hemiptera Cryptocerata. Notes et descriptions d'espèces nouvelles. II. Fam. Belostomidae. *Bull. Soc. Roum. Sci.* **7**: 430–2.

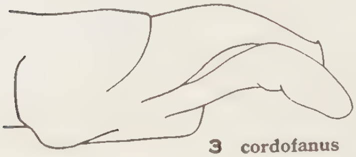
defined, broad yellow stripes; mesosternum before mesocoxae with 2 slightly raised areas; ventral connexival plate I glabrous; profemur short, broad, ratio of greatest length to greatest width 16 : 6·5; profemur deeply emarginate anteriorly just



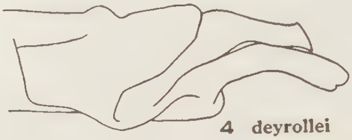
1 indicus



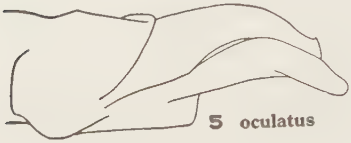
2 insulanus



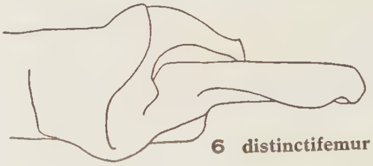
3 cordofanus



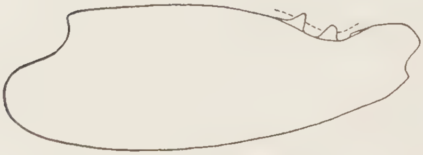
4 deyrollei



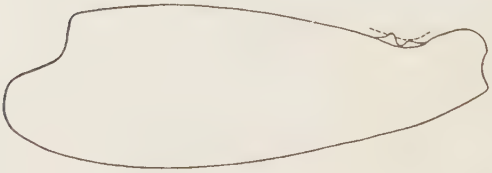
5 oculatus



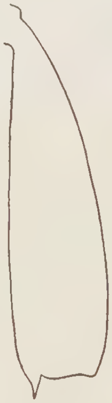
6 distinctifemur



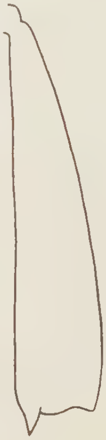
7 distinctifemur



8 insulanus



9 distinctifemur



10 insulanus

Figs. 1–6.—Lateral view of phallus of the six eastern hemisphere species of *Lethocerus*. Figs. 7, 8.—Dorsal view of profemur of *distinctifemur*, sp. nov., and *insulanus*, showing tubercules. The broken lines represent the height of the bristles on the median ridge at the subapical emargination. Figs. 9, 10.—Ventral view of metatibia of same species.

before apex and bearing 2 prominent tubercles on the median ridge at the emargination (Fig. 7); metatibia broad, outer margin curved, ratio of greatest length to greatest width 15 : 4 (Fig. 9); inner ventral angle of metatibia projecting posteriorly into a sharp acuminate spine; metatarsal segment I wider than least interocular distance, ratio 2·5 : 2; male genital plate cleft at apex, female plate narrowly emarginate at apex with a spine at either side of emargination; phallus as in Figure 6.

Types.—Holotype male, Brisbane, Oct. 15, 1941 (B. W. Butler). Two male and 9 female paratypes from the following Australian localities: Brisbane (T. Banner, O. R. Byrne, F. C. Sweeney); 5 miles W. of Gatton, Qld. (K. E. Stager); Gatton, Lawes, Qld. (E. Jones, J. B. Ritson); Monto, Qld. (B. L. Bandidt); Townsville, Qld.; Marlborough, Qld. (K. E. Stager).

The holotype will be deposited in the Queensland Museum. Paratypes will be placed in the following institutions: University of Queensland Collection; University of Kansas Collection; Los Angeles County Museum, California; the David R. Lauck Collection; and the author's collection.

Comparative notes.—The distinctive profemur of this species (Fig. 7) should prevent it from being confused with any other eastern hemisphere *Lethocerus*. In addition, the phallus is very distinct (Fig. 6) and unlike that of any other species (cf. Figs. 1–5). *L. insulanus*, the only species known to occur with *distinctifemur*, has only 1 prominent tubercle on the median ridge of the profemur (projecting above the short bristles on the ridge) (Fig. 8). In *insulanus* the sides of the pronotum are arcuate whereas in *distinctifemur* they are straight. Ventral views of the metatibia of *distinctifemur* and *insulanus* are presented for comparison in Figures 9 and 10 respectively.

Distribution.—*L. distinctifemur* is known only from eastern Australia.

Key to the Eastern Hemisphere Species of the Genus Lethocerus

1. Ventral connexival plate I partially pubescent 2
   Ventral connexival plate I glabrous 4
2. Width of metatarsal segment I (excluding marginal bristles) equal to or less than interocular distance measured at base of clypeus; pronotum with 2 well-defined, diverging, yellow longitudinal stripes 3
   Width of metatarsal segment I greater than interocular distance measured at base of clypeus; pronotum without diverging yellow stripes, unicolorous; Madagascar .... *L. oculatus* (Montandon, 1896)
3. Width of metatarsal segment I equal to interocular distance; yellow stripes of pronotum broad, subequal with width of protibia; length 65–80 mm; south-east Asia, Indonesia, Australia? .... *L. indicus* (Le Peletier & Serville, 1825)
   Width of metatarsal segment I less than interocular distance; yellow stripes of pronotum narrow, much narrower than width of protibia; length 60–65 mm; Africa, south-west Asia .... *L. cordofanus* Mayr, 1853
4. Inner margins of eyes rapidly diverging posteriorly; venter of metatibia with inner angle roundly acuminate, margin of projection bearing short spines; China, Japan, Korea .... *L. deyrollei* (Vuillefroy, 1864)*
   Inner margins of eyes subparallel for most of their length; venter of metatibia with inner angle sharply acuminate, margin of projection not bearing spines 5
5. Ridge separating sulci of profemur bearing a single subapical tubercle; mesosternum with 2 prominent raised areas; Australia, Melanesia .... *L. insulanus* (Montandon, 1898)
   Ridge separating sulci of profemur bearing 2 subapical tubercles; mesosternum without 2 prominent raised areas; Australia .... *L. distinctifemur*, sp. nov.

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* This species was named in honor of Henri Deyrolle but was spelt *deyrolli* in the original description. This was probably a printer's error and is corrected to its proper spelling here.

DISCUSSION

With the description of *L. distinctifemur*, the number of known eastern hemisphere species of *Lethocerus* totals six. The genus *Kirkaldyia* Montandon is here reduced to a synonym of *Lethocerus* because the phallus is not generically distinct from that of the latter. In addition, both have the same type of antennae. The very wide interocular space and the widely diverging eyes of *Kirkaldyia* are the only features which are not typical of *Lethocerus*, but *L. colossicus*, a western hemisphere form, has a head which is intermediate between the extreme type exemplified by *Kirkaldyia* and the rest of the members of the genus.

The phallus of the various eastern hemisphere species of *Lethocerus* are presented in Figures 1-6, and in nearly every case the structure of the phallus is diagnostic for the species. Exceptions are found in *cordofanus* and *oculatus*. *L. oculatus*, which is endemic to Madagascar, is very closely related to *cordofanus* and the two species differ only slightly, even externally.

LIST OF EASTERN HEMISPHERE SPECIES OF THE GENUS LETHOCERUS

The following list includes a critical synonymy. All known published names that apply to the genus in the eastern hemisphere are included, and those that are preceded by a question mark need confirmation through examination of the types:

LETHOCERUS INDICUS (Le Peletier & Serville)

Belostoma indica Le Peletier and Serville, 1825, Encycl. Method. **10**: 272.

LETHOCERUS CORDOFANUS Mayr

Lethocerus cordofanus Mayr, 1853, Verh. zool.-bot. Ges. Wien **2**: 18. Type species.
Belostoma niloticum Stål, 1855, Öfvers. Vetensk.Akad. Förh., Stockh. **11**: 240.
Belostoma patruele Stål, 1855, Öfvers. Vetensk.Akad. Förh., Stockh. **11**: 241 (fide Mayr 1871, Verh. zool.-bot. Ges. Wein **21**: 426).
Belostoma pruinosum Dufour, 1863, Ann. Soc. Ent. Fr. **32**: 381 (fide Mayr 1871, Verh. zool.-bot. Ges. Wien **21**: 426).
Belostoma bispinulosum Dufour, 1863, Ann. Soc. Ent. Fr. **32**: 381–2 (fide Mayr 1871, Verh. zool.-bot. Ges. Wien **21**: 426).
Belostoma lutescens Dufour, 1863, Ann. Soc. Ent. Fr. **32**: 384 (fide Mayr 1871, Verh. zool.-bot. Ges. Wien **21**: 426).
Belostoma niloticum var. *persicum* Montandon, 1898, Bull. Soc. Roum. Sci. **7**: 431.

LETHOCERUS DEYROLLEI (Vuillefroy)

Belostoma deyrolli Vuillefroy, 1864, Ann. Soc. Ent. Fr. **33**: 141.
?*Belostoma aberrans* Mayr, 1871, Verh. zool.-bot. Ges. Wien **21**: 424–5.
?*Belostoma boutareli* Montandon, 1895, Ann. Soc. Ent. Belg. **39**: 471.

LETHOCERUS OCULATUS (Montandon)

Belostoma oculatum Montandon, 1896, Ann. Soc. Ent. Belg. **40**: 517.

LETHOCERUS INSULANUS (Montandon)

Belostoma insulanum Montandon, 1898, Bull. Soc. Roum. Sci. **7**: 431.
Belostoma edentulum Montandon, 1898, Bull. Soc. Roum. Sci. **7**: 432.

LETHOCERUS DISTINCTIFEMUR, sp. nov.

THE GENERA *ELATICHROSIS* HYSLOP AND *LINGANA*, GEN. NOV. (COLEOPTERA: ELATERIDAE)

By A. NEBOISS*

[*Manuscript received February* 17, 1960]

Summary

Species previously referred to the genus *Elatichrosis* Hyslop were found to consist of a number of distinct groups, and the genus is now restricted to that group surrounding the type species *exarata* (Candèze). 13 species are now recognized in the genus *Elatichrosis* s.s., of which nine are described as new, and all are entirely Australian in distribution. The new genus *Lingana* is proposed for the reception of *illita* (Candèze), and one new species from Western Australia. All extra-Australian species are now excluded from *Elatichrosis*.

INTRODUCTION

The genus *Elatichrosis* was first described by Candèze in 1863 under the name of *Chrosis*. It incorporated three Australian species, of which *exarata* (Candèze) and *illita* (Candèze) were then described as new, but the third species, *trisulcata* (Erichson), was abstracted from the genus *Pristilophus*. In subsequent years, Candèze and other authors added further species mainly of New Zealand origin, but as the generic name was preoccupied, Hyslop (1921) changed it to *Elatichrosis*.

In preparing a revision of the Australian species, the conclusion was reached that the genus was not a uniform one. In the first place, there are considerable differences between the Australian species *illita* and the type species *exarata*; furthermore, the extra-Australian species agree neither with *exarata* nor with *illita*. Analysis of the characters of all species listed by Schenkling (1927) clearly indicate that there are a number of distinct groups, which should be raised to generic rank. This was already suggested by Sharp (1881) who, whilst describing *violacea*, stated that "it may prove to be sufficiently distinct structurally, from the other species of *Chrosis* to form a new genus". As the present paper is concerned with the Australian species only, no detailed specific discussion or revision is undertaken of the extra-Australian forms, which, however, must now be excluded from the genus *Elatichrosis*.

Although Candèze described *barbata* as being found in Australia, he noted the lack of exact locality: "Je ne connais pas la provenance exacte de cette espece". Later authors having found the species common in some New Zealand provinces expressed doubt of its presence in Australia (Sharp 1877). Complete absence of *barbata* specimens of Australian origin in all collections examined suggests that it is most improbable that it was ever found in Australia. The species therefore should be omitted from the Australian list.

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* National Museum of Victoria, Melbourne.

A number of institutions and private collectors have made available their material for this study, and they are listed under the following abbreviations:

AM	Australian Museum, Sydney.
BM	British Museum (Natural History), London.
CSIRO	Division of Entomology Museum, C.S.I.R.O., Canberra.
DEI	Deutsches Entomologisches Institut, Berlin.
ETS	Private collection of Mr. E. T. Smith, Melbourne.
FEW	Private collection of Mr. F. E. Wilson, Melbourne.
FH	Private collection of Mr. F. Hallgarten, Melbourne.
FTF	Private collection of Mr. F. T. Fricke, Sydney.
HM	Hobart Museum, Tasmania.
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels.
JA	Private collection of Mr. J. W. T. Armstrong, Nyngan, N.S.W.
JS	Private collection of Mr. J. Sedlacek, San Francisco.
MACL	Macleay Museum, University of Sydney.
MDN	Museum National d'Histoire Naturelle, Paris.
NM	National Museum of Victoria, Melbourne.
QM	Queensland Museum, Brisbane.
QU	Queensland University, Brisbane.
SAM	South Australian Museum, Adelaide.
ZM	Zoologisches Museum, Humboldt University, Berlin.

Colours given in the descriptions are after Ridgway (1912) colour standards.

KEY TO GENERA DISCUSSED

1. Lateral carina of prothorax complete 2
   Lateral carina of prothorax absent or incomplete ....*Elatichrosis* Hyslop
2. Bluntly V- to U-shaped ridge across anterior part of head ....*Lingana*, gen.nov.
   Anterior part of head without such ridge ....Excluded extra-Australian species.

Genus LINGANA, gen.nov.

Figs. 1, 3–6; Plate 1, Fig. 4; Plate 2, Figs. 5 and 6

Type species *Lingana illita* (Candèze), comb.nov.

Head slightly bent downward, sparsely punctate, covered with semidecumbent pubescence; median depression indistinct; bluntly V- to U-shaped ridge across head from base of antennae to anterior margin. Labrum wider than long, anterior margin rounded. Mandibles broad at base, bidentate at apex. Maxillary palps with hatchet-shaped terminal segment. Antennae short, serrate, 1st segment thickened, 2nd very short, 3rd almost as long as 1st, segments 4–10 flattened, triangular, terminal segment elongate.

Pronotum as wide as or wider than long, slightly narrowed anteriorly, sparsely punctate, covered with semidecumbent pubescence; posterior angles short, directed posteriorly or slightly divergent; lateral carina complete; dorsolateral carina short, only slightly longer than posterior angles. Mucro straight.

Scutellum oval or obtusely triangular, convex or flat. Elytra as wide as prothorax; surface smooth, sparsely to moderately punctate; covered with semidecumbent pubescence; striae not depressed, indicated by single rows of punctures only.

Legs slender, tarsi simple, pilose beneath, segments 1–4 diminishing in length, 5th segment about as long as 1st.

Lateral lobes of aedeagus with large rounded lateral hook, median lobe with short, gradually widened furca. Female internal organs of reproduction with large sack-like colleterial glands, and smaller similarly shaped accessory glands; bursa copulatrix covered with numerous spiny plates of variable size.

The generic name is derived from an aboriginal word "ling'an-ling'an", meaning "fish hook", used by natives of Westernport, Vic. The name refers to the large rounded apical hook of lateral lobes.

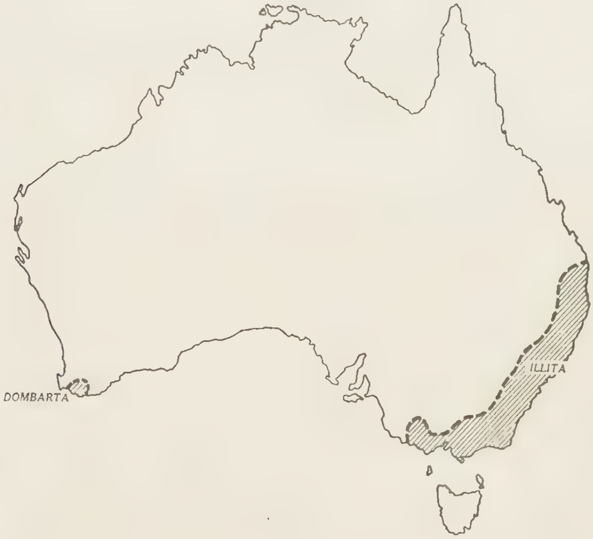

Fig. 1.—Map showing distribution of species of the genus *Lingana.*

Relationship with *Elatichrosis* does not appear to be very close, but that question must be deferred pending further study of other related genera.

According to Wood (1949) the localities are more or less closely associated with dry and wet sclerophyll forest areas.

KEY TO SPECIES OF THE GENUS LINGANA

1. Lateral margins of pronotum usually dark morocco red, elytra gradually narrowed to pointed apex .... *illita* (Cand.)
Two mars orange parallel lines on pronotum some distance inside of lateral margins, elytra broader, rounded towards apex .... *dombarta*, sp.nov.

LINGANA ILLITA (Candèze), comb.nov.

Figs. 3–5; Plate 1, Fig. 4; Plate 2, Fig. 5

Chrosis illita Candèze, 1863, Mem. Soc. Sci. Liege **17**: 187, pl. 2, fig. 7.
Metablax Plasoni Schwarz, 1903, Dtsch. ent. Z. **1903**: 393–4.
Chrosis illita Schwarz, 1906, Dtsch. ent. Z. **1906**: 368.
Elatichrosis illita Schenkling, 1927, Col. Cat. **11**(88): 406.
Elatichrosis illita Neboiss, 1956, Mem. Nat. Mus. Vict. **22**(2): 49.

Candèze, at the time of description, had two specimens for study, one from the Bakewell Collection, the other from the Deyrolle Collection. Label data on two specimens in the IRSNB Collection marked as types do not correspond to the original description and therefore cannot be considered as types; furthermore there is no specimen from the Bakewell Collection nor is there any other specimen labelled as type in the Paris Museum. As the Deyrolle Collection went to the British Museum, it is safe to assume that his specimen of *illita* is in that Institution. Among the material received for study from the British Museum was one ♂ labelled "N.Holl. Victoria. ex Bakewell collection", and another ♂ labelled "Moreton Bay" presumably from the Deyrolle Collection. As the two latter specimens fully agree, and label data corresponds to Candèze's description, the first is now designated as lectotype, the second as lectoparatype of *illita*. Schwarz (1906) reduced his own species *Metablax plasoni*, 1903, to synonmy with *illita*.

Colour varies from morocco red in newly emerged specimens to dark maroon black in fully mature specimens. Lateral margins of pronotum and prosternal episternum of dark morocco red, but occasionally so dark that specimens will appear concolorous. Nitid, sparsely punctate, covered with semidecumbent yellowish pubescence.

Head about as long as wide, median depression shallow and indistinct; ridge across anterior part more or less bluntly V-shaped. Antennae barely reaching posterior angles of prothorax, terminal segment recessed near apex.

Pronotum evenly convex, posterior angles short, straight to slightly divergent, dorsolateral carina short, diverging anteriorly from lateral carina.

Scutellum longer than wide, oval, evenly convex. Elytra gradually narrowed towards more or less pointed apex; striae not depressed, indicated by single rows of punctures; intervals flat, sparsely and irregularly punctate.

Aedeagus slender, lateral lobes with large rounded apical hook, furca short (Fig. 3). Female internal organs of reproduction as in Figures 4 and 5; sides of bursa copulatrix covered with spiny plates of variable size; distinct line of demarcation between larger- and smaller-sized plates on posterior third of bursa.

Length 21–29 mm, width 6–8 mm.

Type locality.—Victoria.

Type location.—BM (location of *M. plasoni* Schw. unknown).

Specimens examined.—Type and 97 others (AM; BM; CSIRO; ETS; FEW; FTF; IRSNB; JA; JS; MACL; NM; QU; SAM; ZM).

Distribution.—Southern Queensland (furthest northern record—Bunya Mts.); New South Wales; Victoria (furthest south-western record—Grampians).

LINGANA DOMBARTA, sp.nov.

Fig. 6; Plate 2, Fig. 6

♀. Superficially very close to *illita*, but easily distinguished by two mars orange parallel lines on pronotum, separated from lateral margin by equidistant marginal line of blackish bay surface colour, which is darker on head and pronotum than on elytra; prosternal episternum mars orange. Nitid, sparsely to moderately punctate, covered with yellowish semidecumbent pubescence.

Head slightly wider than long, median depression indistinct; ridge across anterior part widely U-shaped. Antennae serrate, short, not reaching posterior angles of prothorax, terminal segment indistinctly recessed at apical third.

Pronotum a fraction wider than long, evenly convex, slightly more so than in *illita*; dorsolateral carina short, barely diverging anteriorly.

Scutellum obtusely triangular, flat. Elytra rather broad, rounded towards apex, evenly convex; striae not depressed, indicated by single rows of punctures; intervals flat, moderately and irregularly punctate.

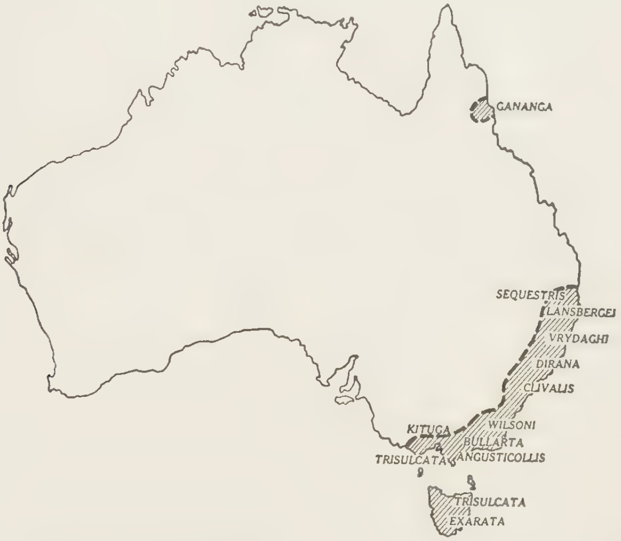

Fig. 2.—Map showing distribution of species of the genus *Elatichrosis* (*E. adusta*, sp.nov. not shown, as no definite localities are available).

General outline of female internal organs of reproduction follow that of *illita*, but differs in detail; spiny plates on sides of bursa copulatrix smaller in size, no distinct line of demarcation present on posterior third of bursa (Fig. 6).

Length 29 mm, width 8·5 mm.

♂. Unknown.

Type material.—Holotype ♀: Warren R., W.A., W. D. Dodd (SAM).

Distribution.—South-western Australia.

The trivial name "dombarta" meaning "single, alone", is derived from an aboriginal word used by natives in south-western Australia.

Genus ELATICHROSIS Hyslop

Figs. 2, 7–40; Plate 1, Figs. 1–3; Plates 2–4, Figs. 7–22

Chrosis Candèze, 1863, Mem. Soc. Sci. Liege **17**: 185 (not Guenée 1845).
Elatichrosis Hyslop, 1921, Proc. U.S. Nat. Mus. **58**: 644.

Type species *Elatichrosis exarata* (Candèze) (designation by Hyslop, 1921).

Head slightly bent downward, about as wide as long, moderately to strongly punctate, frons with triangular median or pair of oval depressions, frontal carina incomplete in middle. Labrum semicircular, wider than long. Maxillary palps with terminal segment hatchet-shaped. Antennae short to moderately long, serrate, 1st segment thickened, 2nd very short, 3rd longer than 2nd, succeeding ones flattened triangular to elongate, last segment recessed at apex.

Pronotum elongate, sparsely to densely punctate, longer than wide, sides more or less parallel; median groove distinct, shallow to deep; lateral grooves less distinct; posterior angles acute, more or less divergent; lateral carina incomplete anteriorly or entirely absent; dorsolateral carina, when present, short, seldom extending further than one-third of length of pronotum.

Shape of scutellum variable. Elytra gradually narrowed or semiparallel, evenly rounded at apex; striae punctate, well defined, moderately deep; intervals flat to slightly convex, punctures usually arranged more or less in rows near striae.

Legs slender, moderately long, tarsi simple, pilose beneath, segments 1–4 diminishing in length, 5th segment long.

Aedeagus with narrow, tapering median lobe, pointed at apex, furca gradually widening, rounded; lateral lobes with apical hooks short, acute, triangular. Female internal organs of reproduction formed by vagina being gradually widened to bursa copulatrix, latter with pair of elongate spiny plates, and few separate, larger or smaller, chitinous spines; colleterial glands short, round; base of spermathecal duct widened to elongate sack, covered with small chitinous spines, and connected to bursa copulatrix by narrow neck.

Key to Species of the Genus Elatichrosis

1. Prothorax with lateral carina entirely absent, median groove closed posteriorly 2
Prothorax with posterior section of lateral carina present, median groove open posteriorly 5

2(1). Third antennal segment about twice as long as 2nd, elytra and abdomen concolorous bay ...... *adusta*, sp.nov.
Third antennal segment only slightly longer than 2nd, abdomen ventrally distinctly darker than elytra 3

3(2). Pronotum minutely and sparsely punctate, median longitudinal band black 4
Pronotum moderately punctate, median band maroon ...... *sequestris*, sp.nov.

4(3). Prosternum mahogany red except black anterior margin and mucro; median groove of pronotum shallow ...... *lansbergei* (Cand.)
Prosternum black, median groove of pronotum deep ...... *gananga*, sp.nov.

5(1). Pronotum covered with semidecumbent to semierect yellowish to brownish pubescence 6
Pronotum covered with conspicuous erect silvery pubescence* 12

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* When examining specimens with damaged or abraded pubescence care should be exercised: both species *wilsoni* and *kituga* could key out to couplet 9. The first, *wilsoni*, being with entirely black pronotum and elytra, or at most with dark reddish toning on the elevated ridges of pronotum and on elytra at either side of scutellum, is readily separable from *exarata* and *trisulcata*; the males of *kituga* have almost entire pronotum black, except for brown posterior angles and sometimes a very narrow lateral margin, which often is quite indistinct, and, furthermore, the anterior part of elytra is kaiser brown, posterior half black; the females of *kituga* if keyed out to *trisulcata* can be separated by the smooth, moderately punctate pronotum and shallow, less-pronounced, widely U-shaped median groove.

6(5). Median groove of pronotum moderately deep to deep, narrow and distinctly V-shaped 7
Median groove of pronotum wide, more or less U-shaped or only for some distance shallowly V-shaped 8

7(6). Pronotum smooth, finely to moderately punctate, median groove moderately deep, dorsolateral carina absent, abdomen and elytra concolorous ....*angusticollis* (Blackb.)
Pronotum rough, densely and deeply punctate, median groove deep, dorsolateral carina present, abdomen distinctly darker than elytra ....*vrydaghi*, sp.nov.

8(6). Pronotum concolorous, or with 3 more or less distinct, black, parallel lines 9
Pronotum with distinct single, black, median line, covering area between lateral grooves 10

9(8). Pronotum orange-rufous to auburn with 3 black parallel lines, ventral surface reddish black to black, darker than elytra ....*trisulcata* (Er.)
Concolorous auburn to dark chestnut, ventral surface not darker than elytra ....*exarata* (Cand).

10(8). Prosternum longitudinally straight 11
Prosternum longitudinally concave ....*clivalis*, sp.nov.

11(10). Elytra with blackish colour on extreme apex only ....*dirana*, sp.nov.
Entire posterior half of elytra black ....*bullarta*, sp.nov.

12(5). Entire elytra black or at most with dark reddish toning on either side of scutellum ....*wilsoni*, sp.nov.
At least anterior half of elytra brown, pronotum with at least posterior angles brown ....*kituga*, sp.nov.

ELATICHROSIS LANSBERGEI (Candèze)

Figs. 7–9; Plate 2, Fig. 8

Chrosis Lansbergei Candèze, 1882, Mem. Soc. Sci. Liege (2) **9**: 97–8.
Elatichrosis lansbergei Neboiss, 1956, Mem. Nat. Mus. Vict. **22** (2): 49.

Head, antennae, scutellum, median band and posterior margin of pronotum, legs, anterior margin of prosternum, mesosternum, metasternum, and abdomen black or very nearly so, remaining parts mars orange to mahogany red. Sexes of similar size and proportions.

Head with pair of faint depressions just above base of antennae, sparsely punctate, interspaces very shiny, pubescence very sparse, dark, and indistinct. Antennae serrate, 2nd and 3rd segments very short, latter only slightly longer, segments 4–10 flattened, somewhat triangular, last segment elongate.

Pronotum sparsely and finely punctate, interspaces shiny, pubescence very sparse, orange, short, almost invisible; anterior margin flatly bilobed; median groove shallow, widely V-shaped, closed posteriorly; lateral carina absent, dorsolateral carina very short, indicated only as indistinct ridge.

Scutellum elevated, broadened posteriorly, surface flat. Elytra slightly wider than prothorax, roundly narrowed toward apex; striae punctate; intervals slightly convex, finely punctate, decumbent mars orange pubescence near striae; posterior half of suture and tips blackish.

Aedeagus as in Figure 7. Structures of bursa copulatrix, and lamina dentata as in Figures 8 and 9 respectively.

Length: ♂ 20–23 mm, ♀ 23–25 mm; width: ♂ 5·5–6·5 mm, ♀ 6·5–7 mm.

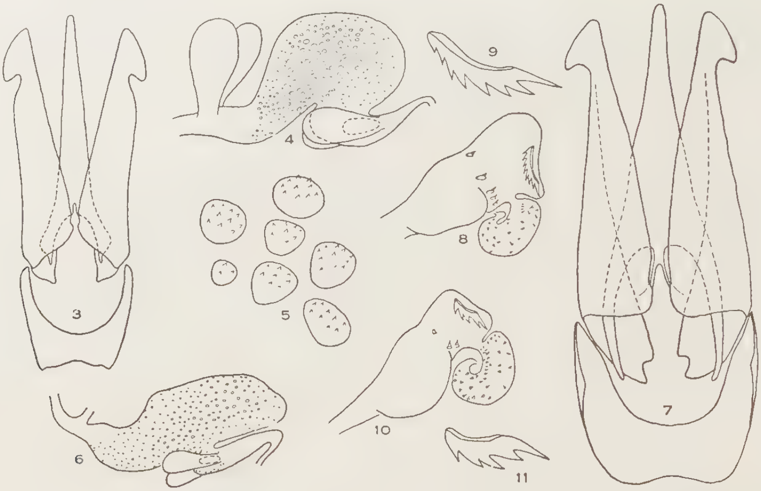
Type location.—MDN.

Type locality.—"New South Wales" (without exact locality).

Specimens examined.—2 ♂♂, 2 ♀♀, National Park, Qld., R. Illidge; 1 ♂, Acacia Plateau, N.S.W., J. Armstrong (JA; NM; QU).

Distribution.—Southern Queensland; northern New South Wales.

The above description was prepared from the specimens collected at the National Park, Qld. 1 ♂ specimen was kindly compared with the type by Dr. A. Villiers of the Paris Museum.



Figs. 3–5.—*L. illita* (Cand.): 3, aedeagus; 4, bursa copulatrix; 5, magnified section of the wall of bursa copulatrix showing spiny plates. Fig. 6.—*L. dombarta*, sp.nov.; bursa copulatrix (holotype). Figs. 7–9.—*E. lansbergei* (Cand.): 7, aedeagus; 8, bursa copulatrix; 9, lamina dentata. Figs. 10, 11.—*E. gananga*, sp.nov: 10, bursa copulatrix (holotype); 11, lamina dentata.

ELATICHROSIS GANANGA, sp.nov.

Figs. 10 and 11; Plate 2, Fig. 9

Pattern of black colour similar to *lansbergei*, with exception that black posterior margin of pronotum is very narrow, prosternum entirely black, and inner margin of prosternal episternum black; remaining coloration orange-rufous.

Head moderately punctate, sparsely covered with fine pubescence, pair of depressions just above base of antennae, latter serrate, not reaching posterior angles of pronotum, 2nd and 3rd segments very short, about equal in length.

Pronotum minutely and sparsely punctate, interspaces shiny, pubescence short and very sparse, visible at higher magnification only, anterior margin bilobed; median groove deep, V-shaped, closed posteriorly; both lateral and dorsolateral carina entirely absent. Prosternum convex longitudinally.

Scutellum raised, semicircular or slightly widened posteriorly. Elytra similar to *lansbergei*, posterior third of suture and tips blackish.

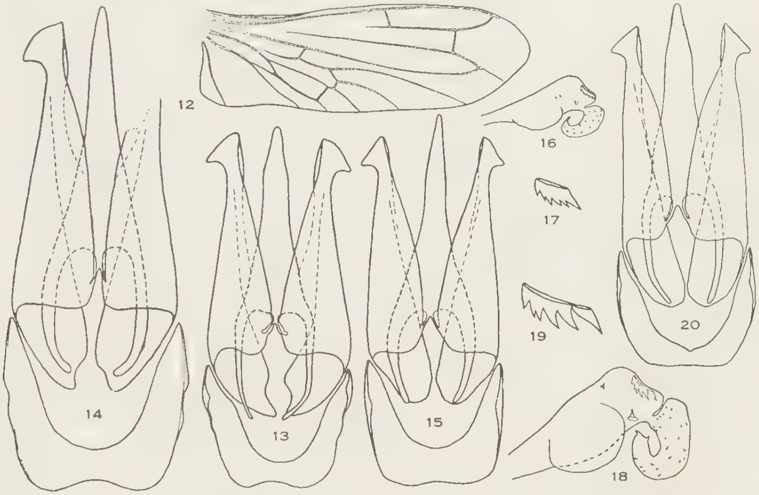
Genitalia follows general generic pattern; bursa copulatrix as in Figure 10, lamina dentata (Fig. 11) shorter, with less spines than in *lansbergei*.

Length: ♂ 19–22 mm, ♀ 22–24·5 mm; width: ♂ 5–6 mm, ♀ 6–7 mm.

Type material.—Holotype ♀, "Kuranda, Qld. March, 1904; F. P. Dodd" (NM); allotype ♂, "Cairns distr. F. P. Dodd" (SAM); 3 ♀♀, 1 ♂ paratypes "Cairns distr. F. P. Dodd" (AM; SAM).

Distribution.—North Queensland.

The trivial name "gananga" meaning "warm" is derived from an aboriginal word used by the natives in eastern Australia.



Figs. 12, 13.—*E. sequestris*, sp.nov.: 12, wing venation (holotype ♂); 13, aedeagus (holotype). Fig. 14.—*E. adusta*, sp.nov., aedeagus (holotype). Figs. 15–17.—*E. angusticollis* (Blackb.): 15, aedeagus; 16, bursa copulatrix; 17, lamina dentata. Figs. 18–20.—*E. vrydaghi*, sp.nov.: 18, bursa copulatrix (paratype); 19, lamina dentata; 20, aedeagus (allotype).

ELATICHROSIS SEQUESTRIS, sp.nov.

Figs. 12 and 13

General appearance of this species is somewhat similar to *lansbergei* and *gananga* but elytra not quite so pointed posteriorly. Pronotal median band broader than in previous two species, but of dark maroon colour instead of black, remaining dorsal surface hazel to sandford's brown.

Head with 2 elongate depressions between eyes; moderately punctate, interspaces shiny; sparsely covered with almost black pubescence. Antennae serrate, in male barely reaching posterior angles of prothorax, in female shorter; 2nd and 3rd segments very short, latter only fraction longer than former, segments 4–10 flattened, last segment elongate.

Pronotum moderately punctate, covered with short decumbent pubescence, anterior margin slightly bilobed, median groove deep, sharply V-shaped, closed posteriorly; lateral and dorsolateral carina absent.

Scutellum elevated, somewhat rounded. Elytra slightly wider than prothorax, evenly rounded towards apex; striae punctate; intervals slightly convex, with minute irregular punctures and rows of orange-rufous decumbent pubescence near striae; anterior two-thirds of median suture blackish, fading posteriorly, posterior third and apex of same colour as elytra.

Aedeagus as in Figure 13.

Length: ♂ 20 mm, ♀ 23 mm; width: ♂ 5·5 mm, ♀ 6·5 mm.

Type material.—Holotype ♂ and allotype ♀ "Lamington National Park, Qld., May, 1955. J. C. Yeo" (QM).

Distribution.—Southern Queensland.

ELATICHROSIS ADUSTA, sp.nov.

Fig. 14; Plate 1, Fig. 2; Plate 2, Fig. 7

Almost concolorous bay to seal brown, median band of pronotum between lateral grooves only slightly darker than remaining part. Female slightly larger than male, but otherwise of similar proportions.

Head moderately punctate, covered with yellowish semidecumbent pubescence; pair of elongate depressions above base of antennae; latter in male barely reaching beyond posterior angles of prothorax, in female slightly shorter; 3rd segment almost twice longer than 2nd.

Pronotum moderately to densely punctate, covered with yellowish semidecumbent pubescence, median groove shallow, closed posteriorly, anterior margin slightly bilobed; lateral carina absent, dorsolateral carina present as elevated ridge only.

Scutellum rounded, slightly elevated. Elytra evenly rounded towards apex, intervals slightly convex; punctation fine, denser near striae, where also most of yellowish decumbent pubescence is placed.

Aedeagus as in Figure 14; female internal organs of reproduction not available for study because of lost abdomen in only female specimen.

Length: ♂ 23·5 mm, ♀ 29 mm; width: ♂ 6·5 mm, ♀ 8 mm.

Type material.—Holotype ♂ "56/85; 68" (no locality) (BM); allotype ♀ "Nov.Holl. *Chrosis aliena* ♀ mihi" (in Janson's handwriting) "Janson's Coll. 1903–130" (BM) (abdomen missing). Specific name *aliena* unpublished.

Distribution.—The only indication is "Nov.Holl." label on one of the type specimens.

ELATICHROSIS ANGUSTICOLLIS (Blackburn)

Figs. 15–17; Plate 4, Figs. 18, 21

Chrosis angusticollis Blackburn, 1900, Trans. Roy. Soc. S.Aust. **24**: 114.
Elatichrosis trisulcata Carter, 1939, Proc. Linn. Soc. N.S.W. **64**: 305.
Elatichrosis trisulcata Neboiss, 1956, Mem. Nat. Mus. Vict. **22**(2): 49.

Carter (1939) placed *angusticollis* as synonym to *trisulcata*, but examination of both holotypes clearly shows that they are two distinct species.

Head, antennae, and central portion of pronotum blackish; remaining parts, including ventral side, auburn to bay.

Head sparsely punctate, covered with sparse yellowish pubescence; median depression indistinct. Antennae serrate, in males reaching beyond posterior angles of prothorax, in females shorter, not reaching posterior angles.

Pronotum semiparallel, sparsely to moderately punctate, covered with sparse yellowish semidecumbent pubescence, median groove narrow, sharply V-shaped, open posteriorly; lateral carina short, barely longer than posterior angles; dorsolateral carina absent; posterior angles sharply divergent in males, less so in females.

Scutellum depressed in middle. Elytra gradually narrowed towards apex, striae well defined, punctate; intervals almost flat, punctate near striae.

Aedeagus similar to that of *exarata* (Fig. 15); female internal organs of reproduction as in Figures 16 and 17.

Length: ♂ 15–20 mm, ♀ 21–28 mm; width: ♂ 3·5–5 mm, ♀ 5–7 mm.

Type material.—Holotype ♂ "6816; H. Vict.; T./Australia; Blackburn Coll.; BM 1910–236/*Chrosis angusticollis,* Blackb." (BM).

Specimens examined.—Type and 17 others (BM; FEW; FTF; NM; SAM).

Distribution.—Victoria.

ELATICHROSIS VRYDAGHI, sp.nov.

Figs. 18–20; Plate 3, Figs. 12, 15

Male resembles *exarata* in shape but easily distinguished by sharply V-shaped median groove of pronotum; females very distinct, considerably larger. Head, prothorax, scutellum, legs, and ventral surface dark claret brown to morocco red, antennae black, elytra sandford's brown to burnt sienna.

Head with median depression, densely and deeply punctate, with dark, fine, and sparse pubescence; antennae serrate, in male just reaching beyond posterior angles of prothorax, in females shorter; 2nd segment shorter than 3rd, segments 4–11 more elongate in male than in female.

Pronotum deeply and densely punctate, giving rough appearance; pubescence sparse yellowish to reddish brown, fine, and hardly visible; anterior margin elevated, ridge-like; median groove deep, sharply V-shaped, open posteriorly; lateral carina slightly longer and more distinct than dorsolateral carina; posterior angles more divergent in males than in females, extreme tip curved upwards and outwards.

Scutellum shield-like, pointed posteriorly, depressed at middle. Elytra flattened, gradually narrowing towards apex in males, subparallel to middle and then narrowing towards apex in females; striae punctate, intervals slightly convex, sparsely and finely punctate, more densely so near striae, and accompanied by fine decumbent golden pubescence.

Male and female genital organs follow general generic characters; aedeagus as in Figure 20, bursa copulatrix and lamina dentata as in Figures 18 and 19 respectively.

Length: ♂ 17 mm, ♀ 26–30 mm; width: ♂ 4 mm, ♀ 7–8·5 mm.

Type material.—Holotype ♀, allotype ♂ "Dorrigo, N.S.W. W. Heron" (SAM); 1 ♀ paratype "Clarence & Macleay River district, N.S.W." (AM); 1 ♀ paratype "National Park, Qld., R. Illidge" (NM).

Distribution.—Southern Queensland and northern New South Wales.

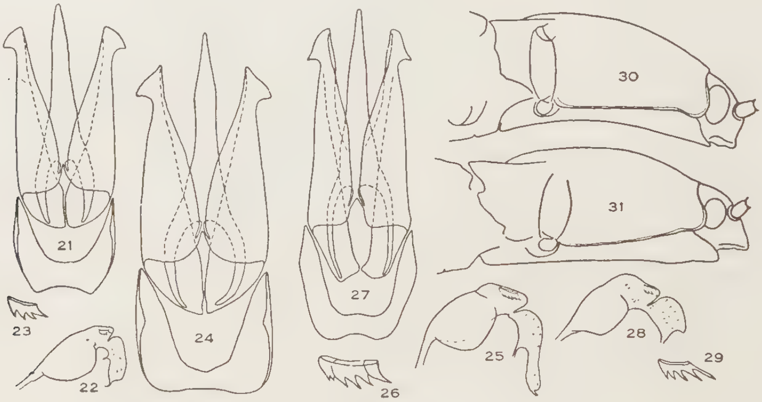
It is a pleasure to name this species after Dr. J. M. Vrydagh, Institut Royal des Sciences de Belgique, Brussels, whose assistance has greatly facilitated the study of Australian Elateridae.

ELATICHROSIS TRISULCATA (Erichson)

Figs. 21–23; Plate 4, Figs. 17, 20

Pristilophus trisulcatus Erichson, 1842, Arch. Naturgesch. **8**(1): 139.
Pristilophus trisulcatus Germar, 1842, Z. Ent. **4**: 92.
Chrosis trisulcata Candèze, 1863, Mem. Soc. Sci. Liege **17**: 186; pl. 2, fig. 10.
Elatichrosis trisulcata Neboiss, 1956, Mem. Nat. Mus. Vict. **22**(2): 49.

Head, antennae, scutellum, 3 parallel lines on pronotum, extreme tip of elytra, legs, and entire ventral surface dark reddish black or black; elytra, anterior and lateral margins and 2 elevated ridges of pronotum orange-rufous to auburn. Males smaller than females, but proportions similar.



Figs. 21–23.—*E. trisulcata* (Er.): 21, aedeagus; 22, bursa copulatrix; 23, lamina dentata. Figs. 24–26.—*E. exarata* (Cand.): 24, aedeagus; 25, bursa copulatrix; 26, lamina dentata. Figs. 27–30.—*E. clivalis*, sp.nov.: 27, aedeagus (paratype); 28, bursa copulatrix (holotype); 29, lamina dentata; 30, lateral aspect of head and prothorax. Fig. 31.—*E. dirana*, sp.nov.: lateral aspect of head and prothorax.

Head deeply and densely punctate, covered with dark pubescence; median depression variable, triangular, sometimes indistinct. Antennae serrate, in males just reaching posterior angles of prothorax, in females shorter, corresponding segments in sexes about the same length, or only slightly longer in males.

Pronotum strongly and densely punctate, covered with short semidecumbent pale yellowish pubescence, median groove widely U-shaped, open posteriorly; lateral carina reaching about half length of prothorax; dorsolateral carina absent, or present only as short indistinct ridge.

Shape of scutellum very variable, generally somewhat rounded, triangular, flat, or depressed. Elytra gradually narrowed towards rounded apex; striae punctate; intervals moderately convex, covered with decumbent pubescence near striae.

Aedeagus as in Figure 21, bursa copulatrix and lamina dentata as in Figures 22 and 23 respectively.

Length: ♂ 13–16 mm, ♀ 17–24 mm; width: ♂ 3–4 mm, ♀ 4·5–6·5 mm.

Type location.—ZM.

Type material.—Type ♂ "16879/*Pristil. trisulcatus* Er. Vandiem. Scheger".

Specimens examined.—Type and 109 others (AM; BM; DAT; HM; ETS; FEW; FH; FTF; MACL; NM; QU; SAM; ZM).

Distribution.—Victoria, Tasmania.

ELATICHROSIS EXARATA (Candèze)

Figs. 24–26; Plate 3, Figs. 11, 14

Chrosis exarata Candèze, 1863, Mem. Soc. Sci. Liege **17**: 186.
Elatichrosis exarata Schenkling, 1927, Col. Cat. **11**(88): 406.
Elatichrosis exarata Neboiss, 1956, Mem. Nat. Mus. Vict. **22**(2): 49.

Concolorous auburn to very dark chestnut; occasionally with legs paler than body, or pronotum with darker grooves. Sexes differing greatly in size and proportions: males rather slender and small, females more robust, distinctly larger.

Head about as long as wide, deeply and densely punctate, covered with yellowish semidecumbent pubescence, median depression very variable in shape and depth. Antennae serrate, in males reaching beyond posterior angles of prothorax, in females much shorter, not reaching posterior angles of prothorax; segments 4–10 about twice as long in males as in females, last segment recessed near apex, more distinctly so in males.

Pronotum strongly and densely punctate, covered with yellowish semidecumbent to semierect pubescence; median groove widely U-shaped, open posteriorly; lateral carina longer than dorsolateral carina, latter only slightly longer than posterior angles. Prosternum in males with anterior margin recurved, higher than rest of prosternal surface; in females anterior third more or less bulging, often higher than anterior margin.

Scutellum in males elongate to triangular, posterior third depressed; in females wide and rounded. Elytra in males gradually narrowing towards apex, in females widest at posterior third, bluntly rounded at apex.

Aedeagus as in Figure 24; bursa copulatrix and lamina dentata as in Figures 25 and 26 respectively.

Length: ♂ 17–21 mm, ♀ 25–31 mm; width: ♂ 4–5 mm, ♀ 6·5–9 mm.

Type location.—BM.

Type material.—Type ♂ "N.Holl./155/Janson Coll. 1903–130/*Chrosis exarata* Cand. ♂ Type. ex coll. de Laferté" (in Janson's handwriting). Type ♀ "N.Holl./154/Janson Coll. 1903–130/*Chrosis exarata* Cand. ♀ Type. ex coll. de Laferté" (in Janson's handwriting).

Specimens examined.—Types and 129 others (AM; BM; DAT; HM; FEW; MACL; NM; QU; SAM).

Distribution.—Tasmania.

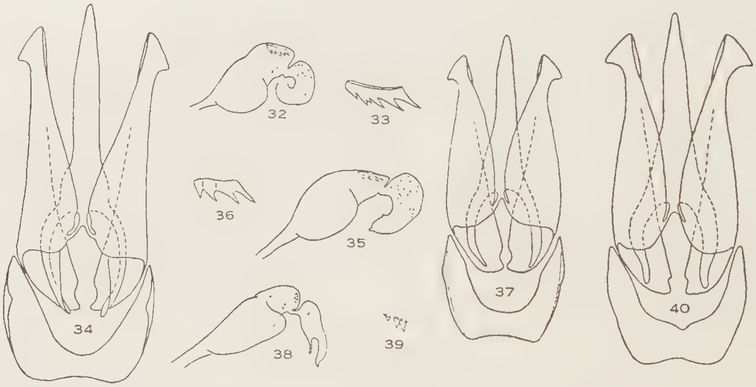
ELATICHROSIS DIRANA, sp.nov.

Figs. 31–33; Plate 2, Fig. 10

♀. Very similar to *clivalis*, but distinguished by parallel-sided elytra, roundly narrowing at apex, and having longitudinally straight prosternum slightly bulging near anterior margin (Fig. 31). General coloration as in *clivalis*; elytra with extreme tip only blackish.

Head moderately punctate with only slight median depression, covered with fine dark pubescence, antennae short, not reaching posterior angles of prothorax; 3rd segment only slightly longer than 2nd.

Pronotum moderately to densely punctate, covered with ferrugineous semi-erect pubescence, median groove widely V-shaped, open posteriorly; lateral and dorsolateral carina distinct, latter shorter. Prosternum straight, slightly bulging anteriorly.



Figs. 32, 33.—*E. dirana*, sp.nov.: 32, bursa copulatrix (holotype); 33, lamina dentata. Figs. 34–36.—*E. bullarta*, sp.nov.: 34, aedeagus (allotype); 35, bursa copulatrix (holotype); 36, lamina dentata. Figs. 37–39.—*E. wilsoni*, sp.nov.: 37, aedeagus (holotype); 38, bursa copulatrix (allotype); 39, lamina dentata. Fig. 40.—*E. kituga*, sp.nov.: aedeagus (holotype).

Scutellum shield-like, flat. Elytra sandford's brown to burnt sienna; semi-parallel, evenly rounded at apex; striae punctate; intervals slightly convex, sparsely punctate, fine ferrugineous decumbent pubescence in rows near striae.

Bursa copulatrix and lamina dentata as in Figures 32 and 33 respectively.

♂. Unknown.

Length 17–23·5 mm, width 4–6 mm.

Type material.—Holotype ♀ "Tubrabucca (Barrington Tops), N.S.W. 4500 ft. Jan. 1948. R.T.M.P." (NM); 5 ♀ paratypes: 1 ♀ "Barrington Tops, N.S.W., 12.xii.1955. R.D." (NM); 2 ♀ "Glen Innes, N.S.W." (AM); 1 ♀ "Barrington Tops, N.S.W., Jan. 1925. Sydney Univ. Zool. Exped." (MACL); 1 ♀ "Mt. Irvine, N.S.W. J. Armstrong" (JA).

Distribution.—New South Wales.

The trivial name "dirana" meaning "mountain" is derived from an aboriginal word used by the natives in eastern Australia.

ELATICHROSIS BULLARTA, sp.nov.

Figs. 34–36; Plate 3, Figs. 13, 16

Shape and colour pattern of pronotum similar to *dirana*, but elytra with anterior half kaiser brown in males, carob brown in females, posterior half black in both sexes; line of demarcation separating both colours more distinct in males than in females; similar colour combination on elytra also found in *kituga* but different colour combination on pronotum makes it easily separable.

Head black, moderately punctate, sparsely pubescent, median depression slight; antennae in male not quite reaching posterior angles of prothorax, in females slightly shorter, 3rd segment only a fraction shorter than 4th segment.

Pronotum moderately punctate, covered with fine semierect yellowish to almost ferrugineous pubescence; median groove U-shaped, open posteriorly; lateral and dorsolateral carina present and distinct.

Scutellum short, widest in middle, depressed. Elytra semiparallel, rounded posteriorly; striae punctate; intervals flat or slightly convex, punctate, and covered with fine decumbent pubescence near striae. Ventral surface entirely black, except kaiser brown to carob brown narrow external margin of prosternal episternum.

Aedeagus as in Figure 34; bursa copulatrix and lamina dentata as in Figures 35 and 36 respectively.

Length: ♂ 21 mm, ♀ 29–30 mm; width: ♂ 5·5 mm, ♀ 7–8 mm.

Type material.—Holotype ♀ "Warburton, Vic., Jan. 1913. H.J.C." (NM); allotype ♂, no locality (NM); 1 ♀ paratype, no locality (QM).

Distribution.—Victoria.

The name is derived from an aboriginal word meaning "big".

ELATICHROSIS CLIVALIS, sp.nov.

Figs. 27–30

Closely resembles *dirana* and *gananga*, but differs from the former by elytra being gradually narrowed towards apex and having longitudinally convex prosternum (Fig. 30); and from latter by pronotum being more closely punctate, median groove shallower, and apex of elytra black. Pattern of black colour similar to *dirana*, being black at apex of elytra, but extending further anteriorly along costal margin and median suture, less pronounced in females.

Head moderately punctate, sparsely covered with dark pubescence, pair of slight depressions near middle; antennae serrate, short, not reaching posterior angles of prothorax, 3rd segment only slightly longer than 2nd.

Pronotum moderately punctate, covered with dark brown semidecumbent to semierect pubescence, median groove shallow, U-shaped, open posteriorly; lateral and dorsolateral carina present, distinct, latter shorter. Prosternum convex longitudinally.

Scutellum shield-like, slightly raised. Elytra gradually narrowed towards apex; striae punctate; intervals slightly convex very sparsely and finely punctate, fine, dark brown decumbent pubescence near striae.

Aedeagus rather slender, lateral lobes with distinctly formed apical hook (Fig. 27); bursa copulatrix and lamina dentata as in Figures 28 and 29 respectively.

Length: ♂ 15–19 mm, ♀ 17–21·5 mm; width: ♂ 4–5 mm, ♀ 4·5–6 mm.

Type material.—Holotype ♀ "Blue Mts., N.S.W." (NM); allotype ♂ "Kurrajong, N.S.W." (NM); 4 ♂♂, 8 ♀♀ paratypes: 1 ♂ "Sydney district, N.S.W. J.J.W." (BM); 1 ♂ "E. Australia" (BM); 1 ♀ "Hazelbrook, N.S.W. J. Armstrong" (JA); 1 ♀ "Kurrajong, N.S.W. Oct. 1931" (AM); 2 ♀ "NSW" (NM); 1 ♀ "Mt. Wilson. N.S.W. F. Fricke" (FTF); 2 ♀ "Blue Mts. N.S.W." (MACL); 1 ♀ "Blue Mts. N.S.W. Dec. 1933. K.K.S." (AM); 1 ♂ "Colo River, N.S.W. C. Deuquet" (JA); 1 ♂ "Upper Williams River N.S.W. Oct. 1926. Lea & Wilson" (SAM).

Distribution.—New South Wales.

ELATICHROSIS WILSONI, sp.nov.

Figs. 37–39

Males entirely black, female similar but with dark reddish toning on elevated part of pronotum and at base of elytra on each side of scutellum.

Head moderately to densely punctate, covered with dark rather long semi-erect to erect pubescence; round to elongate depression on each side just above base of antennae; latter barely reaching beyond posterior angles of prothorax, that of female appear somewhat shorter though incomplete in only specimen.

Pronotum moderately punctate, covered with conspicuous rather long, erect, silvery pubescence; median groove U-shaped, open posteriorly; lateral and dorso-lateral carina distinct, latter only half the length of former.

Scutellum shield-like, depressed at middle. Elytra gradually narrowed towards rounded apex; striae punctate; intervals slightly convex with row of punctures and short, fine semidecumbent pubescence near striae.

Aedeagus as in Figure 37; bursa copulatrix (Fig. 38) with very small lamina dentata (Fig. 39) consisting of few larger spines only.

Length: ♂ 15·5–19·5 mm, ♀ 21·5 mm; width: ♂ 3·5–4·5 mm, ♀ 5·5 mm.

Type material.—Holotype ♂ "Vic. Alps" (FEW); allotype ♀ "Mt. Kosciusko, N.S.W." (FEW); 2 ♂ paratypes "Vic. Alps. H. W. Davey" (NM; SAM).

Distribution.—Southern New South Wales, eastern Victoria.

The species is dedicated to Mr. F. E. Wilson, to whom the author is greatly indebted for assistance and cooperation in many entomological problems.

ELATICHROSIS KITUGA, sp.nov.

Fig. 40; Plate 4, Figs. 19, 22

Head black, moderately punctate, covered with whitish pubescence, median depression slight and indistinct; antennae serrate, black or blackish brown, just reaching beyond posterior angles in males, shorter in females.

Pronotum black, with posterior angles and often also lateral margins kaiser brown in males, and with additional carob brown elevated ridges on either side of median groove in females, moderately punctate, covered with silvery rather long conspicuous erect pubescence, which is easily damaged and then appears almost decumbent in parts; median groove U-shaped, open posteriorly; lateral carina distinct, longer than less distinct dorsolateral carina.

Scutellum elongate, depressed in middle, posterior tip elevated. Elytra roundly narrowed towards apex; males with anterior half kaiser brown, posterior half black, demarcation line distinct; in females almost concolorous carob brown with indistinctly darkened posterior third; striae punctate; intervals slightly convex with decumbent pubescence and punctures near striae. Entire ventral surface black.

Aedeagus as in Figure 40.

Length: ♂ 18–21 mm, ♀ 24–27 mm; width: ♂ 4–5 mm, ♀ 6–7 mm.

Type material.—Holotype ♂, allotype ♀ "Warburton, Vic. Dec. J. E. Dixon" (NM); 12 ♂♂, 4 ♀♀ paratypes: 1 ♂ "Warburton, Vic. 20.xi.1927, F. E. Wilson" (FEW); 8 ♂♂ "Warburton, Vic. 6.xii.1931, F. E. Wilson" (AM; FEW; JA; NM; QM); 1 ♂ "Mt. Donna Buang, Vic. 28.xii.1953, E. T. Smith" (ETS); 1 ♂, 1 ♀ "Mt. Donna Buang, Vic. 14.xii.1930" (BM); 1 ♂, 1 ♀ "Mt. Donna Buang, Vic. 1.i.1944, E. T. Smith" (ETS); 1 ♀, no locality (NM); 1 ♀ "Mt. Donna Buang, Vic. 26.xii.1949, E. T. Smith" (ETS).

Distribution.—Victoria.

The name is derived from an aboriginal word meaning "animal hair" and refers to the hairy appearance of these insects.

Acknowledgments

Acknowledgments are gratefully made to the Institutions and private collectors who made material available to the author. Especial thanks are due to Miss Christine von Hayek, British Museum (Natural History), London; Dr. A. Villiers, Museum National d'histoire Naturelle, Paris; Dr. J. M. Vrydagh, Institut Royal des Sciences Naturelles de Belgique, Brussels; and Dr. K. Delkeskamp, Zoologisches Museum, Humboldt University, Berlin, for their valuable help and cooperation regarding information and loan of types.

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Explanation of Plates 1–4

(Photographs by the author)

Plate 1

The photographs of this plate are stereo-pairs. Structures of the specimens as indicated by arrows will stand out more clearly when viewed under a stereoscope. Numbers apply to each pair

Fig. 1.—*E. exarata* (Cand.), ♂, showing pronotum with posteriorly open median groove.

Fig. 2.—*E. adusta*, sp.nov., ♂ (holotype), showing pronotum with closed median groove.

Fig. 3.—*E. trisulcata* (Er.), ♀. Note absence of lateral carina.

Fig. 4.—*L. illita* (Cand.), ♀. Note distinct ridge between the base of antennae, and presence of lateral carina.

Plate 2

Fig. 5.—*L. illita* (Cand.), ♂, lectotype, "Victoria".

Fig. 6.—*L. dombarta*, sp.nov., ♀, holotype, Warren R., W.A.

Fig. 7.—*E. adusta*, sp.nov., ♂, holotype, no locality.

Fig. 8.—*E. lansbergei* (Cand.), ♀, National Park, Qld.

Fig. 9.—*E. gananga*, sp.nov., ♀, holotype, Kuranda, Qld.

Fig. 10.—*E. dirana*, sp.nov., ♀, holotype, Tubrabucca, N.S.W.

Plate 3

Fig. 11.—*E. exarata* (Cand.), ♂, "Tasmania".

Fig. 12.—*E. vrydaghi*, sp.nov., ♂, allotype, Dorrigo, N.S.W.

Fig. 13.—*E. bullarto*, sp.nov., ♂, allotype, no locality.

Fig. 14.—*E. exarata* (Cand.), ♀, type, "N.Holl."

Fig. 15.—*E. vrydaghi*, sp.nov., ♀, holotype, Dorrigo, N.S.W.

Fig. 16.—*E. bullarta*, sp.nov., ♀, holotype, Warburton, Vic.

Plate 4

Fig. 17.—*E. trisulcata* (Er.), ♂, Drouin, Vic.

Fig. 18.—*E. angusticollis* (Blackb.), ♂, Warburton, Vic.

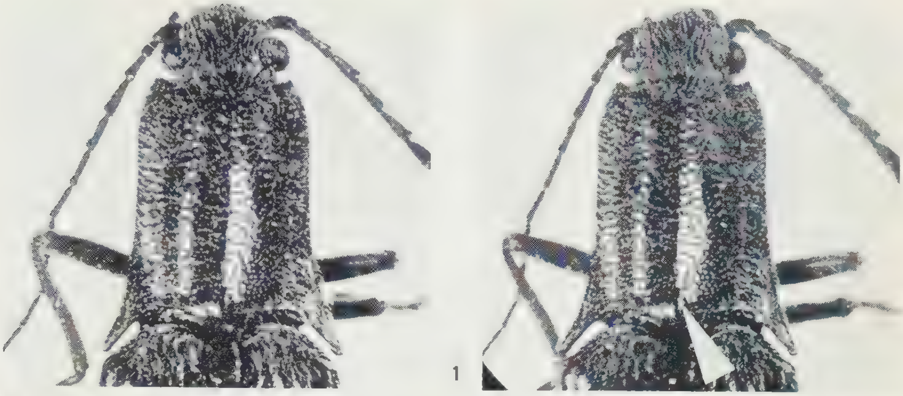
Fig. 19.—*E. kituga*, sp.nov., ♂, holotype, Warburton, Vic.

Fig. 20.—*E. trisulcata* (Er.), ♀, Warburton, Vic.

Fig. 21.—*E. angusticollis* (Blackb.), ♀, Gippsland, Vic.

Fig. 22.—*E. kituga*, sp.nov., ♀, allotype, Warburton, Vic.

THE GENERA ELATICHROSIS AND LINGANA



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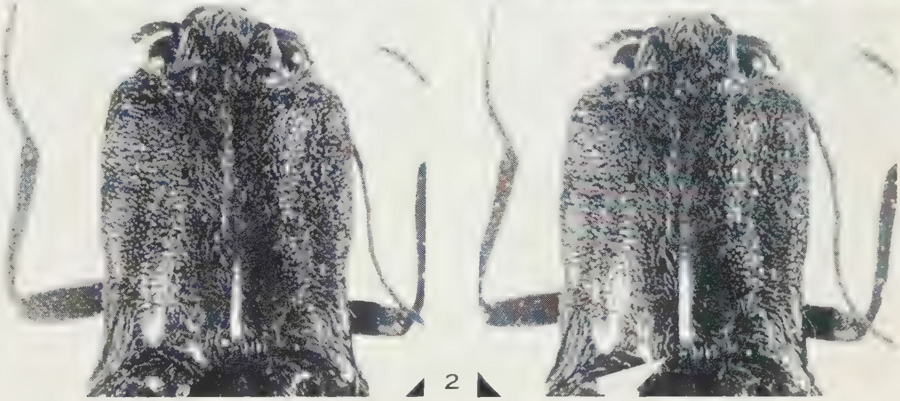

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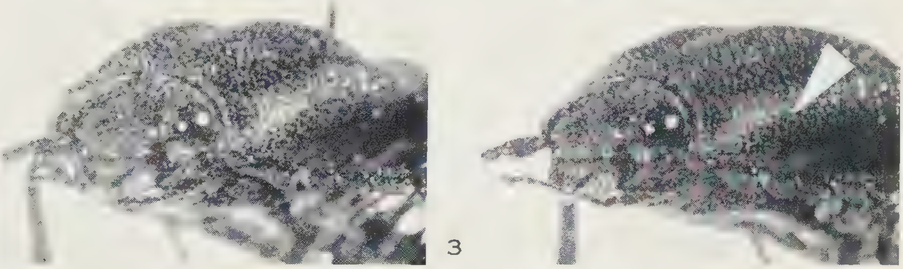

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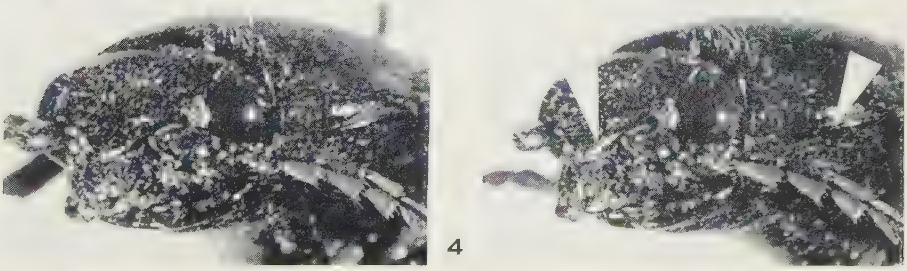

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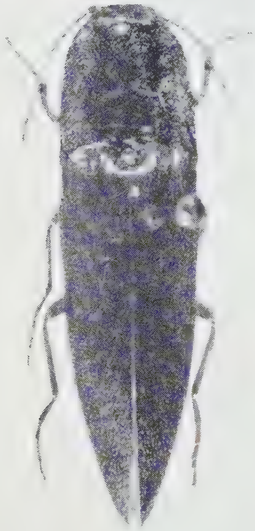

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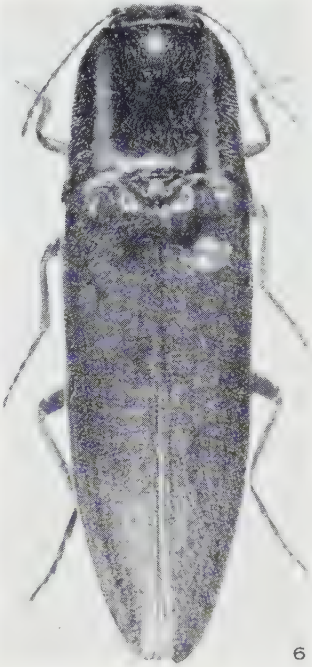

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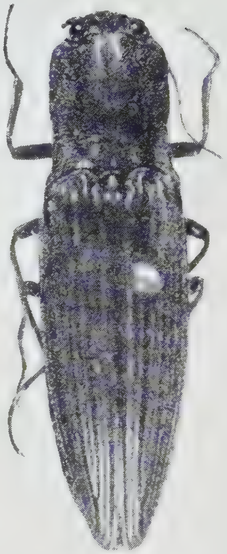

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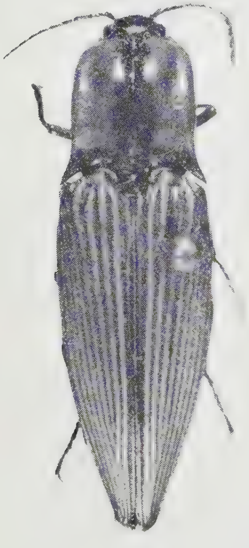

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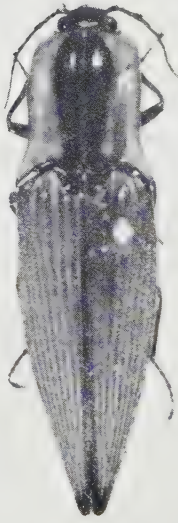

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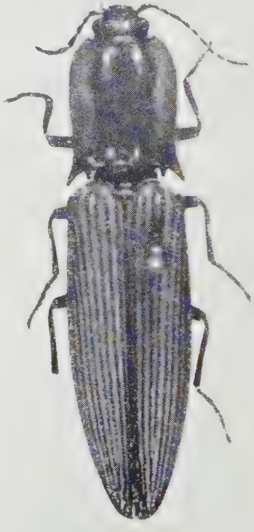

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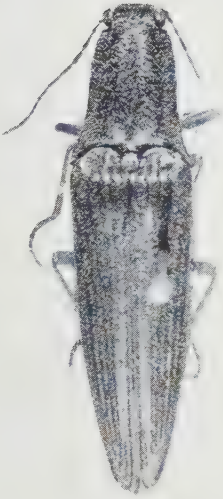

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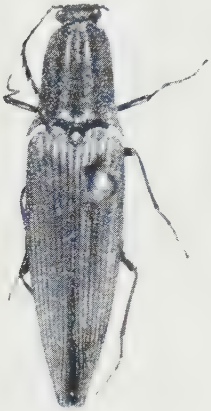

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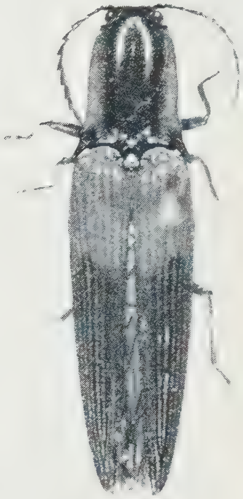

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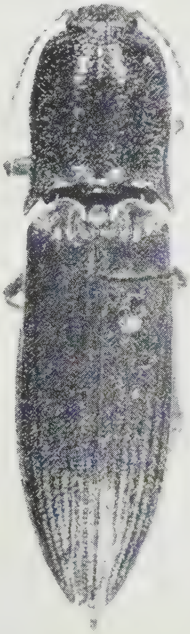

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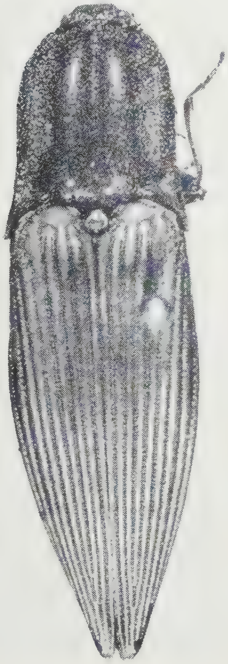

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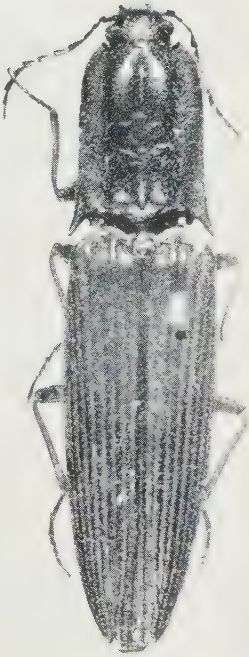

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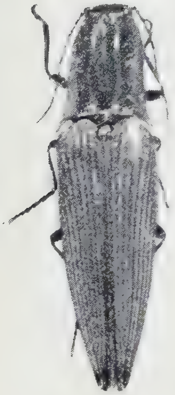
THE GENERA ELATICHROSIS AND LINGANA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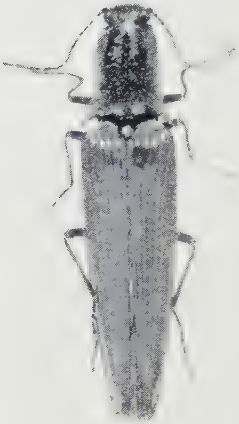
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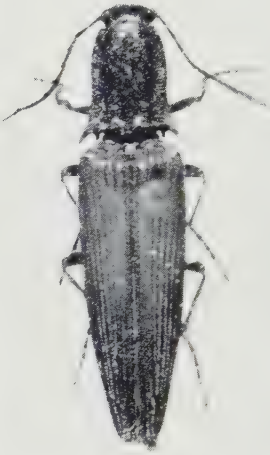
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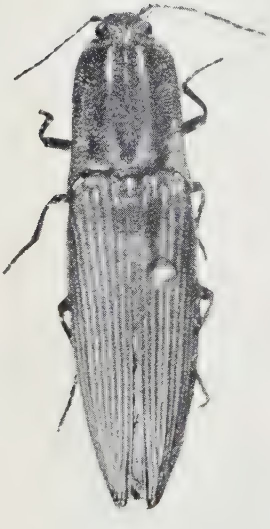
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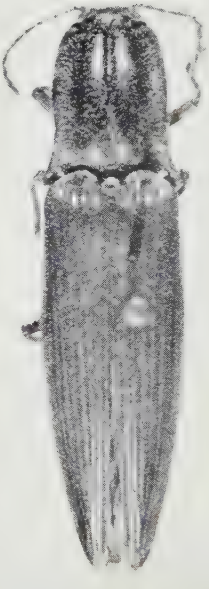
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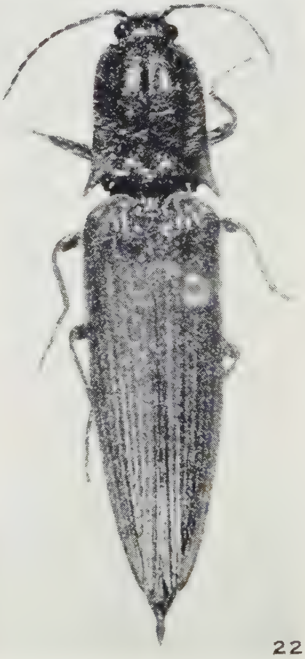
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A REVISION OF THE AUSTRALIAN STEM BORERS HITHERTO REFERRED TO *SCHOENOBIUS* AND *SCIRPOPHAGA* (LEPIDOPTERA: PYRALIDAE, SCHOENOBIINAE)

By I. F. B. Common*

[*Manuscript received February* 10, 1960]

Summary

The Australian pyralid stem borers of Gramineae, Cyperaceae, and Juncaceae, previously assigned to *Schoenobius* Duponchel and *Scirpophaga* Treitschke, are here referred to six genera.

Scirpophaga Treit.—Eight species are recognized: *S. chrysorrhoa* Zeller, *S. phaedima*, sp. nov., *S. limnochares*, sp. nov., *S. xantharrenes*, sp. nov., *S. imparella* (Meyrick), *S. helodes*, sp. nov., *S. percna*, sp. nov., and *S. ochroleuca* (Meyrick). Though some of these bear a superficial resemblance to the true rice stem borers, the genus includes species whose larvae attack sedges (Cyperaceae).

Helonastes, gen. nov.—The genus is based on a new species, *H. acentrus*, associated with *Eleocharis* (Cyperaceae) in central Queensland.

Niphadoses, gen. nov.—The genus is erected to include three new Australian species, *N. palleucus*, which is associated with cultivated rice in north-western Australia, *N. elachia*, and *N. hoplites*, together with *N. chionotus* (Meyrick) from New Guinea and *N. gilbiverbis* (Zeller) from India.

Catagela Walker.—A new species, *C. adoceta*, from northern Australia, is described.

Tryporyza gen. nov.—The genus is established to receive the two important stem-borer pests of cultivated rice, *Tipanaea innotata* Walker from south-east Asia and northern Australia and *Chilo incertulas* Walker from south-east Asia, previously referred to *Scirpophaga* and *Schoenobius* respectively. Also included are *Scirpophaga butyrota* Meyrick from New Guinea and *Schoenobius melanostigmus* Turner from the Cape York Peninsula. It is suggested that *T. innotata* already occurred in northern Australia before European settlement.

Tipanaea Walker.—The genus is restricted to the single Australian species, *T. patulella* Walker, associated with Juncaceae.

Genitalic and other structures used to distinguish these genera are discussed. The genitalia of both sexes and the wings of the Australian species are figured, and keys to the genera and species are included.

Introduction

Recent unsuccessful attempts to identify a pyralid stem-borer pest of experimental and commercial rice crops in north-western Australia and the Northern Territory drew attention to the chaotic state of the systematics of this group of Lepidoptera, not only in Australia, but throughout the Old World. Jepson (1954) also encountered this problem when reviewing the literature on the biology and control of the top and paddy borers. More recently, Martin (1958) clarified the synonymy of the important Indian rice stem borer, *Schoenobius incertulas* (Walker),

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and another species. A thorough re-evaluation of the genera to which the various pest species have been assigned is long overdue, but cannot be accomplished satisfactorily without a detailed study of the extensive world fauna. It has not been possible to attempt such a task in this paper.

The present study is confined to a critical revision of the Australian species previously assigned to *Schoenobius* Duponchel and *Scirpophaga* Treitschke, relating it wherever possible to the limited data available on species from abroad. This has necessitated a study of the type species of a series of Old World genera including *Schoenobius*, *Scirpophaga*, *Donacaula* Meyrick, *Acentropus* Curtis, *Tipanaea* Walker, *Catagela* Walker, *Apurima* Walker, *Rupela* Walker, *Panalipa* Moore, and *Microschoenis* Meyrick. These are among the nominal genera referred to the Schoenobiinae by Munroe (1958).

Ten species have previously been ascribed to the Australian fauna. Hampson (1895) recognized only three Australian species. To *Scirpophaga* he referred *patulella* Walker (with *exsanguis* Meyrick as a synonym) and *imparellus* Meyrick, while to *Schoenobius* he referred *adjurella* Walker, including Australia in its distribution. Meyrick (1882) had added *ochroleuca* to *Scirpophaga*, but Hampson (1895) could not place this species. Turner (1911) identified specimens from Darwin as *Schoenobius chionotus* Meyrick, a New Guinea species, and in 1922 described two further species *Schoenobius melanostigmus* and *S. crossostichus*. Later Meyrick (1934) described *Schoenobius caustodes* from Sydney and finally Turner (1937) added *Scirpophaga haplosticha* from Cape York.

In the present study, only 4 of these 10 species are recognized as valid Australian representatives of the group. Australian specimens identified by Hampson (1895) as *adjurella* Walker are referred to *chrysorrhoa* Zeller (Martin 1958), while a specimen identified by Turner (1911) as *chionotus* Meyrick has proved to be a new species of *Scirpophaga*. *Schoenobius crossostichus* Turner belongs to the Crambinae and should be referred to the genus *Chilotraea* Kapur (1950) (new combination). *Scirpophaga haplosticha* Turner is congeneric with, and probably identical with, *Ramila stenopteralis* Hampson and, although belonging to the Schoenobiinae, does not belong to the *Scirpophaga* group of genera. *Schoenobius caustodes* Meyrick likewise does not belong to this group and may be one of the Scopariinae, although the presence of a ventral brush on the seventh abdominal segment of the male suggests a relationship with the Schoenobiinae.

In the present paper 16 species are included in the Australian fauna, 10 of which are described as new. They are referred to 6 genera: 8 species to *Scirpophaga*, 3 to *Niphadoses*, gen. nov., 2 to *Tryporyza*, gen. nov., and 1 each to *Tipanaea*, *Catagela*, and *Helonastes*, gen. nov.

Characters used for Delineating the Genera and Species

The Schoenobiinae are distinguished from the remaining Pyralidae primarily by the presence of vein 1*A* in the forewing. This vein is often well developed only towards the wing margin.

The proboscis, in the genera related to *Schoenobius* and *Scirpophaga*, is present though not strongly developed and all have porrect labial palpi. In the forewing veins R_2 and R_5 arise separately from the cell. The females all have a dense tuft of long deciduous hair-scales surrounding the lobes of the ovipositor, some of which are used by the ovipositing moth to cover the egg masses.

In several genera, the seventh abdominal sternite in the male bears a large flattened tuft of scales which extends over the eighth sternite and conceals a rounded membranous area of the integument. Its function is not known. The rear margin of this membranous area bears another flattened tuft of shorter scales and various sclerotized areas of the eighth sternite are associated with it. In longitudinal section the seventh and eigth abdominal segments of *Scirpophaga xantharrenes*, which had been fixed in alcoholic Bouin medium, showed no trace of a sense organ associated with either of these scale tufts or with the membranous area of the eighth sternite.

The 2 or more bristles which comprise the frenulum of the female in most Lepidoptera are, in all but three Australian species of the *Scirpophaga* group, fused together, forming a single stout bristle, very similar to that in the male. However, a frenulum of 2 closely appressed bristles is found in *Scirpophaga chrysorrhoa*, and *S. limnochares*, and in *Tryporyza innotata*, as well as in the Asian *T. incertulas*. Evidently the condition of the frenulum is not a reliable generic character.

The genitalia in both sexes provide the most useful characters for the differentiation of genera and show that previous definitions of genera such as *Schoenobius* and *Scirpophaga* are quite inadequate. Useful characters for the separation of the species are also provided by the genitalia. Some intraspecific variation in detail of the genitalic characters have been noted, but once recognized this does not prevent a precise use of these characters.

In the male, the uncus and the gnathos are usually of similar shape, the former drawn out to a slender rounded apex and curved downwards, while the arms of the latter unite medially to form a similar slender structure which curves upwards towards the apex of the uncus. The anus appears between these two structures. The shape of the uncus and gnathos are of value in differentiating genera and species.

The dorsum of the tegumen of the male genitalia has a sclerotized thickening of characteristic shape, which seems to be of generic significance. In *Scirpophaga* it is roughly rectangular or H-shaped; in *Helonastes* it consists of 2 more or less parallel bands; in *Catagela* and *Tipanaea* it is Y-shaped; in *Niphadoses* it is roughly X-shaped; while in *Tryporyza* it is rather indeterminate but more or less triangular in shape. Beneath the tegumen, anterior to the gnathos, is a pair of sclerotized arms of considerable taxonomic significance. In the natural position they hang straight downwards, but are usually bent either inwards or outwards when the specimen is mounted on a microscope slide. They do not appear to represent the arms of a transtilla, the term used for them by Forbes (1923), but are outgrowths of the lateral portions of the tegumen. In this paper, they are referred to as the subteguminal processes. In *Scirpophaga* and *Helonastes* they are flattened clavate structures, often with a serrated or indented edge; in *Niphadoses* they have smooth margins, somewhat similar to the more reduced form in *Scirpophaga*; in *Catagela* they are flattened processes tapering to a curved point; in *Tryporyza* they are in the form of a large single or bifid hook; while in *Tipanaea* they are reduced to very small slightly sclerotized lobes.

The juxta, which is usually a simple plate, and the anellus which is membranous and finely spined, do not usually provide useful generic characters. However, in the Holarctic genus *Donacaula*, there is a strong pointed projection near the apex of the juxta, and in *Catagela* the juxta is produced into a very long tapering projection.

In the female, the genitalic characters are also of value in defining genera. In *Scirpophaga*, the ductus bursae has a heavily sclerotized lining and the spherical corpus bursae has thick walls, densely lined with minute spines. A somewhat similar but less strongly sclerotized lining is found in the ductus bursae of *Niphadoses*, but the walls of the corpus bursae are thinner and the internal spining less dense. In *Tryporyza*, the poorly differentiated ductus bursae is membranous and the internal spining of the corpus bursae is still less dense. In *Catagela* and *Tipanaea* the ductus bursae is only slightly thickened, while the corpus bursae is membranous without any spining.

Distribution of the Species in Australia

The Australian species of the *Scirpophaga* group of genera are clearly of Oriental origin. Most of them are confined to the northern half of the continent, but a few extend southwards along the east coast. Of the 16 species recorded here, only four occur in the coastal or subcoastal areas of northern New South Wales, two in southern New South Wales and Victoria, and one in Tasmania. None have been collected in South Australia or in south-western Australia. More intensive collecting in northern Australia, especially in the Northern Territory and in the Cape York Peninsula and the Gulf Country of Queensland, will certainly bring to light many further species.

Key to the Australian Genera of the Scirpophaga Group

1. Male genitalia with subteguminal processes a pair of single or bifurcate hooks; female genitalia with ostium very broad, with thickened and wrinkled walls .... *Tryporyza*, gen. nov.
Male and female genitalia not so 2

2(1). Subteguminal processes in male a pair of flattened rounded structures, sometimes with serrate margin; corpus bursae of female densely lined with short spines, at least in anterior half 3
Male and female genitalia not so 5

3(2). Aedoeagus of male without cornuti; ductus seminalis of female leaving ductus bursae at its junction with corpus bursae .... *Helonastes*, gen. nov.
Aedoeagus of male with well-developed cornuti; ductus seminalis of female leaving ductus bursae near middle or nearer ostium than corpus bursae 4

4(3). Aedoeagus of male with cornuti a horn and 2 or 3 thorns; dorsal thickening of tegumen H-shaped; labial palpus medium to short, with appressed scales; forewing with *Sc* and R_1 separate .... *Scirpophaga* Treit.
Aedoeagus of male with cornuti a horn, 2 small thorns, and a series of short spines; dorsal thickening of tegumen X-shaped; labial palpus long, with expanded scales; forewing with *Sc* and R_1 almost invariably anastomosing .... *Niphadoses*, gen. nov.

5(2). Male genitalia with juxta produced into a long tapering projection; labial palpus in both sexes very long, more than three times diameter of eye .... *Catagela* Walk.
Male genitalia with juxta not produced; labial palpus in both sexes short, little more than diameter of eye .... *Tipanaea* Walk.

Genus SCIRPOPHAGA Treitschke

Scirpophaga Treitschke, 1832, Schmetterlinge Europa ix, 1, p. 55.

Types species *Scirpophaga praelata* Scopoli, from Europe.

Proboscis short, weak; antenna in male finely serrate and ciliate, in female much shorter, with short cilia; labial palpus smooth-scaled, short (Fig. 2*A*) usually shorter in female, apical segment much shorter than second, porrected; maxillary palpi short, expanded with scales apically. Forewing (Fig. 1*A*) with R_1 from two-thirds to three-quarters cell, R_2 from near upper angle of cell, R_3 and R_4 stalked from just before upper angle, R_4 to costa near apex, R_5 from near upper angle of cell to termen near apex, M_1 and R_5 approximated at base but separate, M_2 and M_3 approximated at base, M_3 from lower angle of cell, Cu_1 from before angle and Cu_2 from two-thirds to four-fifths cell. Hindwing (Fig. 1*A*) with *Rs* and M_1 connate from upper angle, M_3 from lower angle of cell, Cu_2 from before two-thirds cell. Abdomen of male with posterior margin of seventh sternite with flattened tuft of scales projecting over eighth sternite; abdomen of female with seventh tergite bearing a large and dense tuft of long, deciduous hair-scales, many of which are used by the ovipositing female to cover egg masses.

Male genitalia.—Uncus tapering to rounded point; gnathos arms united in centre and drawn out to a tapering rounded point, similar in general shape to uncus; tegumen with dorsal thickening rectangular or H-shaped, ventrally with a pair of large flattened, clavate processes, often with serrated margin; volva simple, more or less quadrate; anellus membranous, clothed with fine spines; aedoeagus elongate, nearly straight, slightly expanded towards distal orifice; vesica armed with 2 or 3 heavily sclerotized thorns and a thickened horn.

Female genitalia.—Ostium broad, membranous, lined with minute spines; ductus bursae broad with a heavily sclerotized lining throughout its length; corpus bursae nearly spherical, without signum, but with thick walls densely lined with fine spines.

The above definition of the genus *Scirpophaga* is based on the type species and a series of Australian species, some of which have genitalia extremely similar to those of the type. One of the Australian species, *S. chrysorrhoa*, is widely distributed in both the Oriental and Australian Regions. No doubt numerous Oriental species remain to be checked critically.

Several of the species are sexually dimorphic, with dark-coloured males and white or nearly white females. It has therefore been a matter of some difficulty correctly associating the sexes. Both sexes of *S. praelata*, on the other hand, are white. It was thought formerly (e.g. Jepson 1954) that the sexually dimorphic species belonged to *Schoenobius*, whereas *Scirpophaga* contained species that were white in both sexes. Hence, for example, the white female of *S. chrysorrhoa* was originally described in *Scirpophaga*, whereas the ochreous grey male was described on two separate occasions in *Schoenobius*.

In Australia the genus may be divided into two fairly well defined species groups, the *praelata* group and the *imparella* group. The former is represented by *S. chrysorrhoa*, *S. phaedima*, *S. limnochares*, and *S. xantharrenes*, while the latter

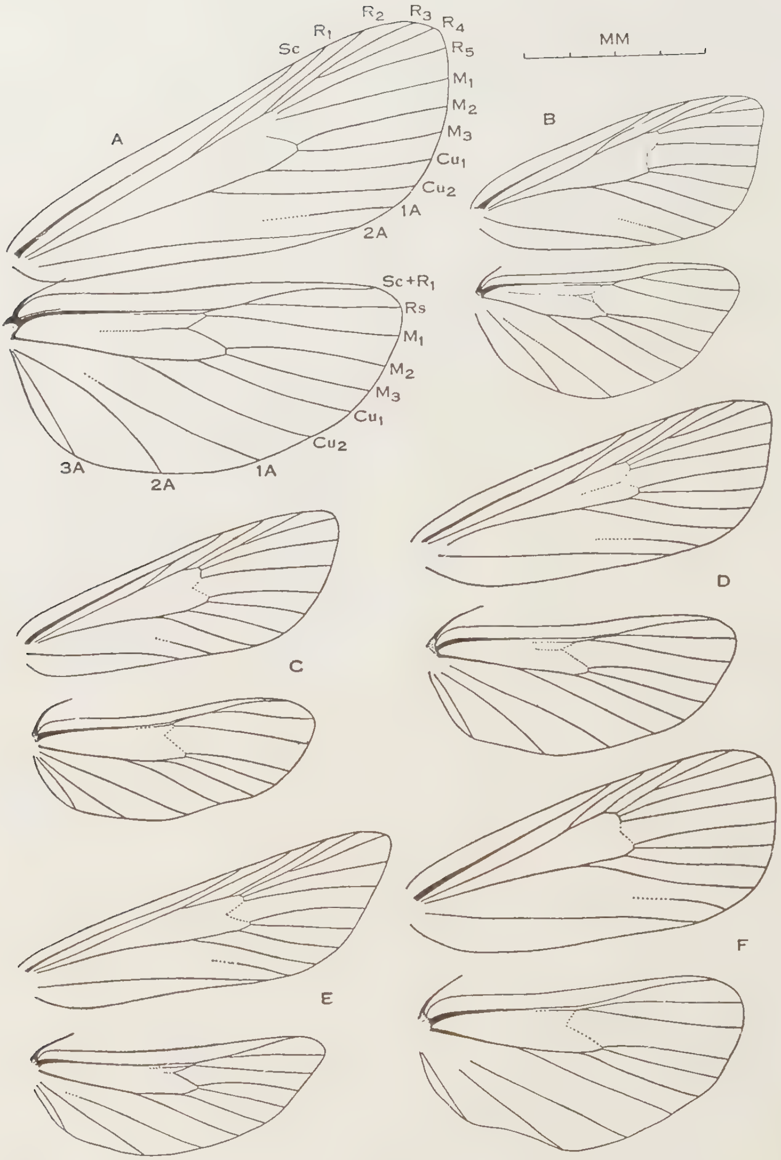

Fig. 1.—Wing venation of: *A*, *Scirpophaga praelata* Scop., male, Macedonia; *B*, *Tipanaea patulella* Walk., male, Canberra; *C*, *Niphadoses palleucus*, sp. nov., paratype male, 25 miles N. of Gin Gin, Qld.; *D*, *Tryporyza innotata* (Walk.), male, Ivanhoe, north-western Australia; *E*, *Catagela adoceta*, sp. nov., paratype male, 25 miles N. of Gin Gin, Qld.; *F*, *Helonastes acentrus*, sp. nov., paratype male, Dingo, Qld.

contains *S. imparella*, *S. helodes*, and *S. percna*. The *praelata* group is distinguished by the presence of 2 strong thorns in the male aedoeagus and the relatively short labial palpi in the female. In the *imparella* group, there are 3 strong thorns in the male aedoeagus and the labial palpi are about equal in length in both sexes. *S. ochroleuca* stands quite alone and there is little doubt that, when the male is available for study, the species will have to be separated generically. It has therefore been omitted from the key.

The species of *Scirpophaga* can be distinguished from all other Australian genera by the genitalia. The shape of the dorsal thickening of the tegumen, the shape of the subteguminal processes, and the armature of the aedoeagus are usually diagnostic. In the female, the sclerotized lining of the ductus bursae and the spherical, thick-walled, and densely spined corpus bursae are reliable characters.

As the name of the genus implies, the larvae probably all feed within the stems of sedges. The Australian species have not been reared, but some have been taken commonly resting on the stems of *Scirpus* and *Eleocharis* (Cyperaceae) growing in permanent freshwater swamps, and these plants will doubtless prove to be their hosts.

KEY TO AUSTRALIAN SPECIES OF THE GENUS SCIRPOPHAGA

Males

1. Both forewing and hindwing shining white .... *S. phaedima*, sp. nov.
   Forewing not shining white 2
2(1). Forewing light orange-yellow .... *S. xantharrenes*, sp. nov.
   Forewing not so 3
3(2). Forewing dull ochreous grey or pale ochreous 4
   Forewing fuscous or dark fuscous 5
4(3). Forewing dull ochreous grey, without markings .... *S. limnochares*, sp. nov.
   Forewing pale ochreous, with faint subterminal oblique line and spots fuscous .... *S. chrysorrhoa* Zell.
5(3). Uncus and gnathos strongly produced, the latter tapering gently ...... *S. percna*, sp. nov.
   Uncus and gnathos less strongly produced, the latter tapering more abruptly 6
6(5). Gnathos arms uniting abruptly in median line, subteguminal processes with numerous scale-like projections .... *S. imparella* (Meyr.)
   Gnathos arms uniting obliquely in median line, subteguminal processes without scale-like projections .... *S. helodes*, sp. nov.

Females

1. Underside of forewing white 2
   Underside of forewing with at least basal half strongly suffused with dark fuscous 4
2(1). Upperside of forewing shining white .... *S. limnochares*, sp. nov.
   Upperside of forewing shining ochreous white 3
3(2). Anal tuft ochreous .... *S. chrysorrhoa* Zell.
   Anal tuft ochreous white .... *S. percna*, sp. nov.
4(1). Forewing white with black costa, anal tuft light orange-yellow .. *S. xantharrenes*, sp. nov.
   Forewing white, ochreous grey, or fuscous, without black costa 5
5(4). Abdomen white, with white anal tuft .... *S. helodes*, sp. nov.
   Abdomen largely white, anal tuft ochreous grey or fuscous .... *S. imparella* (Meyr.)

Scirpophaga chrysorrhoa Zeller

Figs. 4*A*, 4*B*, 7*B*; Plate 1, Figs. 1 and 2

Scirpophaga chrysorrhoa Zeller, 1863, Chilonidarum et Crambidarum genera et species, p. 1; Martin, 1958, Bull. Ent. Res. **49**: 189, figs. 4, 8, pl. vi, figs. 5, 6.

Schoenobius brunnescens Moore, 1888, Descriptions of new Indian lepidopterous insects from the collection of . . . W. S. Atkinson. Heterocera, part 3, p. 225. (Type locality: Calcutta, India; holotype ♂ in British Museum (Natural History), genitalia slide No. Pyralidae 2466.)

Schoenobius celidias Meyrick, 1894, Trans. Ent. Soc. Lond. **1894**: 475. (Type locality: south-east Borneo; holotype ♂ in British Museum (Natural History), genitalia slide No. Pyralidae 2264.)

Type.—The holotype female labelled "chrysorrhoa, Java, Tengstr." is in the British Museum (Natural History) (genitalia slide No. Pyralidae 2263). Mr. D. S. Fletcher (personal communication) states that the label is in Zeller's handwriting.

Male.—Head and antenna ochreous or greyish ochreous; labial palpus greyish ochreous, in length about 1·5 times diameter of eye. Thorax ochreous or greyish ochreous; legs ochreous or greyish ochreous, anterior legs and middle tarsi suffused with fuscous, posterior, anterior, and middle legs ochreous greyish, the anterior legs and middle tarsi suffused with fuscous, posterior legs pale ochreous. Abdomen pale ochreous, some golden scales on dorsum of basal segments. Forewing ochreous, sometimes suffused with grey, 3 fuscous spots on fold, at one-fifth, two-fifths, and just beyond one-half, and another at end of cell; an indistinct fuscous line from costa just before apex extending obliquely inwards to lower angle of cell; fuscous dots on termen at end of veins; cilia ochreous or greyish ochreous. Hindwing whitish in basal half, ochreous or greyish ochreous in distal half; cilia whitish, pale ochreous towards apex.

Female.—Head and antenna white; labial palpus white, slightly suffused with pale ochreous, in length about 1·3 times diameter of eye. Thorax white; legs white, anterior and middle legs and posterior tarsi suffused with fuscous. Abdomen white, some golden scales on dorsum of 2 basal segments, anal tuft large, spreading, ochreous. Forewing shining white or ochreous white, underside white, cilia white. Hindwing white; underside white; cilia white; frenulum a pair of closely appressed bristles.

Male genitalia.—Uncus short; gnathos arms uniting abruptly; subteguminal processes large, flattened, with coarsely serrated margin; aedoeagus long, slender, armed with 2 strong thorns and a short, slightly curved horn.

Female genitalia.— Ductus bursae with strong swelling near ostium, in which sclerotized lining forms almost globular expansion.

Expanse.—Male 21·2–35·8 mm, female 22·7–45·5 mm.

Specimens examined.—43 ♂♂, 64 ♀♀.

Distribution.—Northern Australia, extending southwards along the eastern coast to northern New South Wales. Martin (1958) records it also from India, East Pakistan, Ceylon, Andaman I., Thailand, Borneo, and southern China, while the type is from Java. Specimens from the following localities have been examined by the author: QUEENSLAND: Ayr, Bowen, Brisbane, Cairns, Cape York, Dunk I., Halifax, Mackay, Stewart R., Silver Plains (Cape York

Peninsula), Townsville. NEW SOUTH WALES: Brunswick Heads, Burringbar. WESTERN AUSTRALIA: Ivanhoe. NORTHERN TERRITORY: Bathurst I., Darwin, Groote Eylandt, Humpty Doo, Marrakai, Mary R., Melville I., Stapleton.

Comments.—The male can be readily distinguished from other Australian species by the genitalia and the forewing. It belongs to the species group with 2 large thorns in the aedoeagus, and is thus separated from *S. imparella*, *S. helodes*, and *S. percna*. From *S. phaedima* it may be distinguished by the colour of the forewings and the size. The light orange-yellow and ochreous greyish forewings respectively in *S. xantharrenes* and *S. limnochares* both without markings, contrast strongly with the marked forewings of *S. chrysorrhoa*. The subteguminal processes in these two species are without or with only very slight marginal serrations. The labial palpi of *S. limnochares* are also shorter.

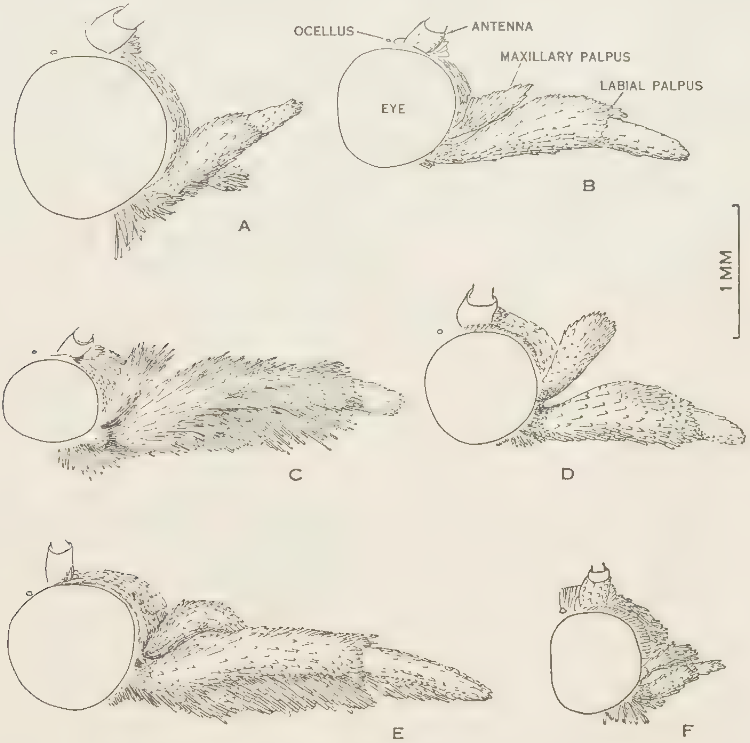

Fig. 2.—Head and palpi of: *A*, *Scirpophaga praelata* Scop., male, Macedonia; *B*, *Tryporyza innotata* (Walk.), male, Ivanhoe, north-western Australia; *C*, *Niphadoses palleucus*, sp. nov., holotype male, 25 miles N. of Gin Gin, Qld.; *D*, *Helonastes acentrus*, sp. nov., holotype male, Dingo, Qld.; *E*, *Catagela adoceta*, sp. nov., holotype male, 25 miles N. of Gin Gin, Qld.; *F*, *Tipanaea patulella* Walk. male, Canberra.

In the female, the absence of dark fuscous suffusion beneath the forewings separates *S. chrysorrhoa* from *S. xantharrenes*, *S. imparella*, and *S. helodes*, while the ochreous anal tuft separates it from *S. limnochares* and *S. percna*, in which the tuft

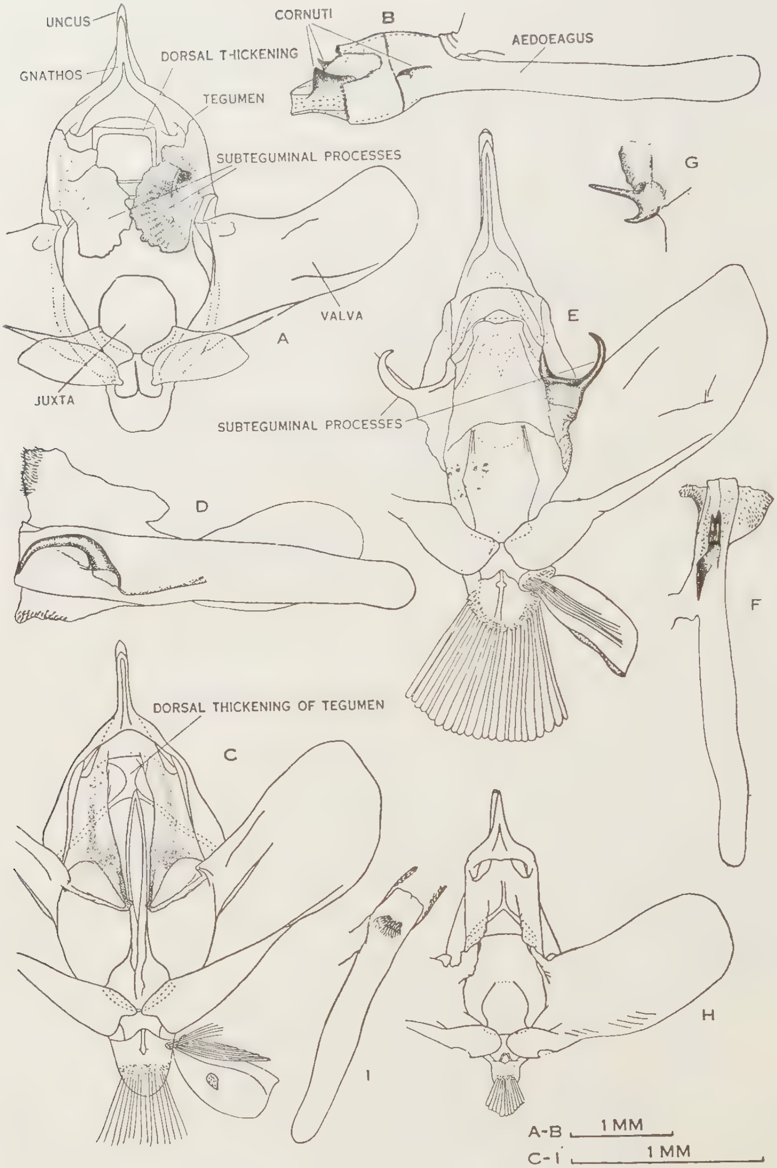

Fig. 3.—Male genitalia of: *A*, *B*, *Scirpophaga praelata* Scop., Macedonia; *C*, *D*, *Catagela adoceta*, sp. nov., holotype, 25 miles N. of Gin Gin, Qld.; *E*, *F*, *Tryporyza innotata* (Walk.) Ivanhoe, north-western Australia; *G*, *T. incertulas* (Walk.) (right subteguminal process), India; *H*, *I*, *Tipanaea patulella* Walk. Crows Nest, Qld.

is white or nearly so. It is similar in size both to *S. limnochares* and *S. percna*, but, whereas in the former the forewings are shining white, in *S. chrysorrhoa* and *S. percna* they usually have a slightly ochreous suffusion.

Australian male specimens of *S. chrysorrhoa* have been identified as *Schoenobius adjurellus* (Walker) by Hampson (1895) and they stood under this name in the collection of the late A. J. Turner. The females were identified by Turner as *S. imparella*. Martin (1958) discussed the synonymy of the species and compared northern Australian specimens with the holotype in the British Museum. Males and females have been taken by the author in close proximity to one another at Burringbar in northern New South Wales and at Humpty Doo in the Northern Territory. At Burringbar the dominant sedge growing in the permanent freshwater swamps where the species occurred was *Cladium articulatum* R.Br. (Cyperaceae) but at Humpty Doo both sexes were taken at rest on *Eleocharis dulcis* (Burm. f.) Trin. ex. Hensch. (Cyperaceae).

SCIRPOPHAGA PHAEDIMA,* sp. nov.

Figs. 4*C*, 4*D*; Plate 2, Fig. 1

Types.—Holotype male (genitalia slide No. P15), labelled "P. Darwin, Jan. 09, F. P. Dodd", in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Holotype male.—Head and antenna white; palpi white, suffused with pale ochreous on outer surface, labial palpus in length 1·6 times diameter of eye. Thorax white; legs white, anterior and middle legs with outer surface suffused with light fuscous. Abdomen white, dorsum suffused with ochreous yellow, especially towards base. Forewing and cilia very pale ochreous white, shining, without markings; underside white, with light fuscous suffusion. Hindwing and cilia white; underside white, with light fuscous suffusion, especially towards costa and apex. Expanse 22·4 mm.

Male genitalia (*holotype*).—Uncus short, gnathos arms uniting abruptly; subteguminal processes large, flattened, rounded, with strongly indented margin; aedoeagus slender, expanded towards apex, armed with 2 thorns and small straight horn.

Expanse.—Male 17·6–22·4 mm.

Specimens examined.—3 ♂♂.

Distribution.—Northern Territory and the Cape York Peninsula, Qld. Apart from the holotype, the author has examined two male specimens from Silver Plains, Cape York Peninsula (J. L. Wassell), also in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Comments.—The male may be distinguished from the males of other known Australian species by its uniform white forewing. It belongs to the *S. praelata* group of species. The genitalia are rather similar to those of *S. chrysorrhoa*, having subteguminal processes with indented margin.

The female has not yet been recognized.

* φαιδιμος, shining.

SCIRPOPHAGA LIMNOCHARES,* sp. nov.

Figs. 4*E*, 4*F*, 7*C*; Plate 1, Figs. 5 and 6

Types.—Holotype male (genitalia slide No. P123) and three paratype males labelled "Coraki, N.S.W., 10 Jan. 1958, I. F. B. Common", allotype female (genitalia slide No. P133), six male and four female paratypes with same label data but collected March 12, 1958. Allotype female and two paratype males also bear the

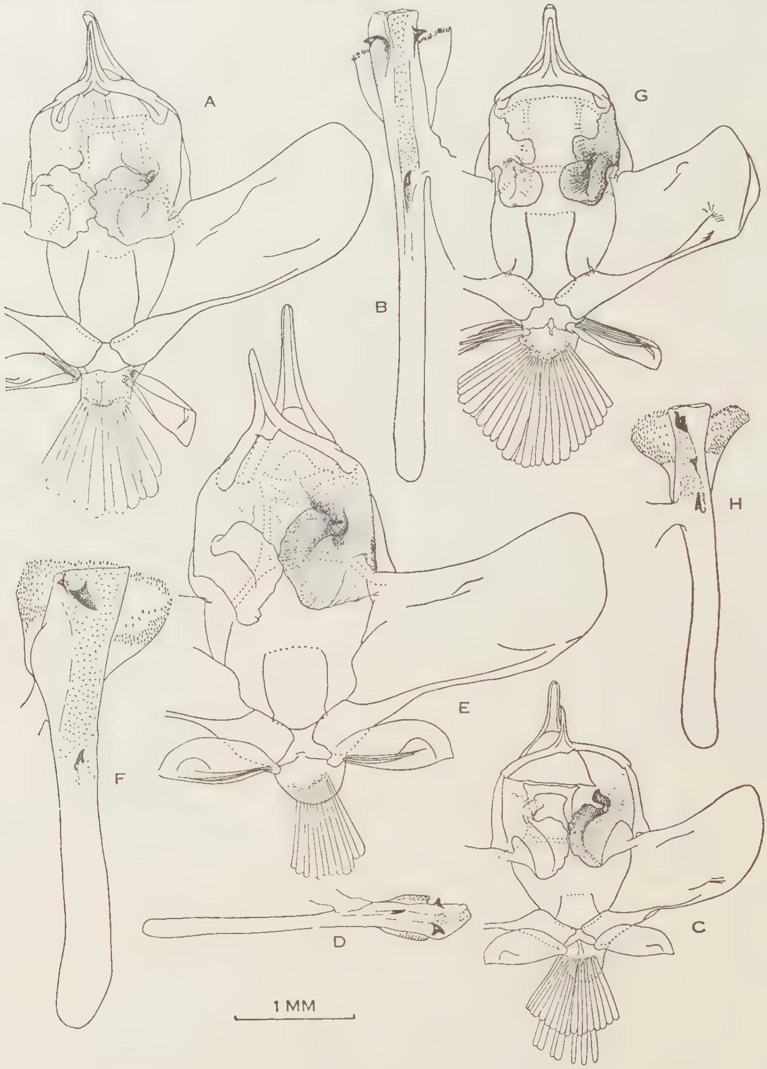

Fig. 4.—Male genitalia of: *A*, *B*, *Scirpophaga chrysorrhoa* Zell., Humpty Doo, N.T.; *C*, *D*, *S. phaedima*, sp. nov., holotype, Darwin; *E*, *F*, *S. limnochares*, sp. nov., holotype, Coraki, N.S.W.; *G*, *H*, *S. xantharrenes*, sp. nov., holotype, 12 miles E. of Duaringa, Qld.

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* λιμνοχαρης, delighting in marshes.

label "at rest on *Scirpus validus* Vahl.". Holotype, allotype, and seven paratypes in the Division of Entomology Museum, C.S.I.R.O., Canberra; one male and one female paratype deposited in each of the following museums: British Museum (Natural History), Australian Museum, Sydney, and South Australian Museum, Adelaide.

Holotype male.—Head and antenna pale ochreous; labial palpus pale ochreous with some brownish lateral suffusion, in length 1·3 times diameter of eye. Thorax pale greyish ochreous; anterior and middle legs greyish ochreous, suffused with fuscous, posterior legs whitish, tarsi with slight fuscous suffusion. Abdomen pale ochreous, some golden brown scaling of the dorsum, especially of basal segments. Forewing greyish ochreous, without markings; base of costa with slight fuscous suffusion; cilia dull ochreous. Hindwing and cilia whitish in basal half, dull ochreous in distal half. Expanse 34·8 mm.

Allotype female.—Head and antenna white; labial palpus white, in length 1·3 times diameter of eye. Thorax white; legs white, tarsi fuscous with white apices, anterior femora and tibiae suffused with fuscous. Abdomen white, some pale yellow scaling on dorsum of basal two segments, anal tuft white. Forewing and cilia shining white; underside white; hindwing and cilia shining white; underside white; frenulum a pair of closely appressed bristles. Expanse 37·9 mm.

Male genitalia (*holotype*).—Uncus moderate, gnathos arms uniting obliquely, gradually tapering; subteguminal processes large, flattened, with slightly sinuate margin; aedoeagus long, broader towards apex, armed with 2 strong thorns and a short, slightly curved horn.

Female genitalia (*allotype*).—Ductus bursae broadened near ostium, sclerotized lining forming a funnel-shaped expansion at entrance.

Expanse.—Male 27·9–34·8 mm, female 29·7–45·4 mm.

Specimens examined.—11 ♂♂, 21 ♀♀.

Distribution.—Coastal and subcoastal central and southern Queensland and far northern New South Wales. Specimens have been examined from the following localities: QUEENSLAND: Brisbane, 15 miles E. of Duaringa, 25 miles N. of Gin Gin, Isis Junction, 20 miles S. of Maryborough. NEW SOUTH WALES: Coraki, Tweed R.

Comments.—The unicolorous greyish ochreous forewing in the male serves to distinguish it from other Australian species. The genitalia, with cornuti represented by only 2 strong thorns and a horn, at once places it in the *S. praelata* group of species, while the gnathos tapers less abruptly than in *S. chrysorrhoa*, *S. xantharrenes*, and *S. phaedima*. With its shining white wings, both above and beneath, the female is only likely to be confused with *S. chrysorrhoa*, in which the anal tuft is ochreous, instead of white.

One male of this species and two females from Brisbane stood in the collection of the late A. J. Turner, along with females of other species, under the name of *S. imparellus*. The author was able to associate the sexes with confidence when the type series was collected on a freshwater permanent swampy creek near Coraki, N.S.W. In January and March, specimens of both sexes were taken at light and at rest on *Scirpus validus* Vahl. and on *S. mucronatus* L. Some larval damage was observed in stems of the latter. Egg masses, covered with whitish hair scales, matching those of the female anal tuft, were observed at this locality and also near Maryborough and at Isis Junction, Qld. At the last two localities in March only females were taken, at rest on *Scirpus littoralis* Schrad.

SCIRPOPHAGA XANTHARRENES,* sp. nov.

Figs. 4*G*, 4*H*, 7*D*; Plate 1, Figs. 3 and 4

Types.—Holotype male, allotype female (genitalia slides Nos. P124 and P134), 16 male and 17 female paratypes labelled "12 mls. E. of Duaringa, Q., 18 Mar. 1958, I. F. B. Common"; 3 male and 3 female paratypes labelled "15 mls. E. of Duaringa, Q., 4 April 1957, I. F. B. Common"; 2 male and 2 female paratypes labelled "Dingo. Q., 19 Mar. 1958, I. F. B. Common, at rest on *Eleocharis dulcis*"; 1 male and 2 female paratypes labelled "Hedlow Ck., near Yeppoon, Q., 22 Mar. 1958, I. F. B. Common"; 3 males and 1 female paratypes labelled "Rockhampton, Q., 17 Mar. 1958, I. F. B. Common". Holotype, allotype, and 38 paratypes in the Division of Entomology Museum, C.S.I.R.O., Canberra. Two paratypes, a male and a female, deposited in each of the following museums: British Museum (Natural History), Canadian National Collection, Ottawa, Canada; Queensland Museum, Brisbane; Australian Museum, Sydney; National Museum of Victoria, Melbourne; and South Australian Museum, Adelaide.

Holotype male.—Head and antenna light orange-yellow (Ridgway 1912), a fringe of white scales surrounding eye; labial palpus light orange-yellow, suffused with fuscous, in length 1·5 times diameter of eye. Thorax light orange-yellow, legs white, outer surface of anterior and middle legs and posterior tarsi suffused with dark fuscous. Abdomen whitish, some orange-yellow scaling on dorsum of basal segments. Forewing light orange-yellow without markings, costa fuscous, cilia ochreous yellow; underside fuscous, cilia ochreous yellow. Hindwing whitish towards base, shading to grey in distal half, cilia white near base, ochreous grey towards apex; underside whitish near base, remainder fuscous, cilia white near base, ochreous white towards apex. Expanse 31·2 mm.

Allotype female.—Head and antenna white, labial palpus white, in length 1·3 times diameter of eye. Thorax white, legs white, outer surface of anterior and middle legs and posterior tarsi suffused with fuscous. Abdomen white, suffused with ochreous above, anal tuft light orange-yellow. Forewing white, without markings, the dark underside of wing tending to show through, especially in basal and costal areas and along veins, costa dark fuscous; underside fuscous in basal three-quarters, especially on veins, area between subcostal vein and costa white; distal quarter and cilia white. Hindwing and cilia white; underside white, suffused with fuscous along costa, in cell, and along veins; frenulum a single stout bristle. Expanse 37·6 mm.

Male genitalia (*holotype*).—Uncus short, gnathos arms uniting abruptly; subteguminal processes moderate with plain margin; aedoeagus slender, only slightly expanded towards apex, armed with 2 thorns and an almost straight horn.

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* *ξανθος*, yellow; *ἀρρενης*, male.

Female genitalia (*allotype*).—Ductus bursae broad, except at junction of corpus bursae where it is narrower, sclerotized lining not expanded towards ostium, with a more heavily sclerotized subcylindrical thickening, with pointed anterior end, between junction of ductus seminalis and ostium.

Expanse.—Paratypic series: male 25·1–31·2 mm; female 29·4–40·3 mm.

Specimens examined.—26 ♂♂, 25 ♀♀.

Distribution.—Known so far from central Queensland, from Yeppoon westwards to Dingo, and from Humpty Doo, N.T.

Comments.—The shining orange-yellow colour of the forewing in the male clearly distinguishes it from other Australian species. The male genitalia too are distinctive, including the shape of the subteguminal processes, the shape of the valva, the shape of the aedoeagus and the relative size of its thorns. It belongs to the *S. praelata* group of species in which the cornuti of the aedoeagus are represented by 2 thorns and a horn.

In the female, the fuscous underside imparts a rather bluish hue to the white upperside. The dark fuscous costa of the forewing and the orange-yellow anal tuft are also distinctive.

Both sexes were taken at light and also, near Duaringa and Dingo, at rest on the stems of *Eleocharis dulcis* growing in permanent freshwater swamps and in an artificial railway lagoon. Egg masses, covered with orange-yellow hair-scales, matching the anal tuft of the female, were also present on this plant, which will doubtless prove to be its host.

SCIRPOPHAGA IMPARELLA (Meyrick)

Figs. 5*A*, 5*B*, 7*E*; Plate 1, Figs. 7 and 8

Schoenobius imparellus Meyrick, 1878, Proc. Linn. Soc. N.S.W. **3**: 176.

Scirpophaga imparella (Meyrick) Hampson, 1895, Proc. Zool. Soc. Lond. **1895**: 914.

Types.—Meyrick's original series is in the British Museum (Natural History). Mr. D. S. Fletcher has kindly selected a male labelled "Sydney, N. S. Wales, 8/3/78", which is hereby designated as the lectotype.

Male genitalia.—Uncus moderately tapered; gnathos arms uniting abruptly; subteguminal processes moderate, rounded, with finely serrated margin and scale-like projections on outer surface; aedoeagus with cornuti represented by 3 thorns and a slightly curved horn.

Female genitalia.—Ductus bursae expanded between junction of ductus seminalis and ostium, lining more strongly sclerotized in this region.

Expanse.—Male 24·2–33·6 mm; female 34·8–48·0 mm.

Specimens examined.—36 ♂♂, 30 ♀♀.

Distribution.—Known from the northern tablelands and coastal New South Wales south of Port Macquarie and from eastern Victoria. The author has examined specimens from the following localities: NEW SOUTH WALES: Bateman's Bay, Colo R., Glen Innes, Port Macquarie, Raymond Terrace, Sydney, 22 miles E. of Tenterfield. VICTORIA: Carlisle R., Cowes, Dutson, Sale.

Comments.—Meyrick's original description is satisfactory. He states that the forewing of the female is "satiny-white, sometimes more or less strongly suffused throughout with whitish ochreous". This is true of the specimens taken by the author on the Colo R., about 30 miles from the type locality, and also of specimens from north of Sydney and from Victoria. However, a series of 14 females taken, together with males, at Bateman's Bay, N.S.W., included two with uniformly fuscous forewings and most of the remainder with forewings uniformly brownish ochreous (Plate 1, Fig. 8) or strongly suffused with brownish ochreous. The genitalia of both sexes were similar to those from the Colo R.

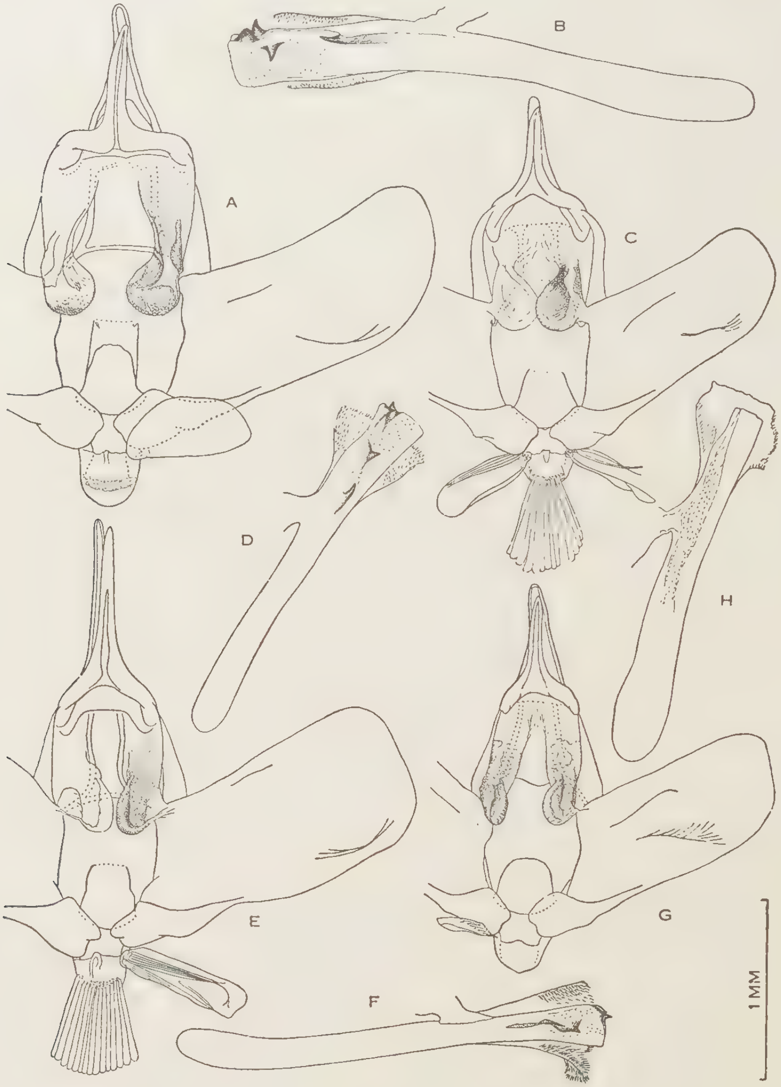

Fig. 5.—Male genitalia of: *A*, *B*, *S. imparella* (Meyr.), Colo R., N.S.W.; *C*, *D*, *S. helodes*, sp. nov., holotype, Dingo, Qld.; *E*, *F*, *S. percna*, sp. nov., holotype, Darwin; *G*, *H*, *Helonastes acentrus*, sp. nov., holotype, Dingo, Qld.

At Bateman's Bay, the dominant sedge on the freshwater lagoon where the specimens were taken was *Cladium articulatum*, which is probably the host of the species in that area. At Raymond Terrace, at Glen Innes, and near Tenterfield, specimens were taken at rest on *Eleocharis sphacelata* R.Br., the only sedge observed. Egg masses covered with whitish ochreous hair-scales, similar to those of the anal tuft of the females from these localities, were also common on this host. There is little doubt, therefore, that this sedge is the host in these areas. Neither of these observations supports Meyrick's statement that "the larva feeds in the cylindrical stem-like leaves of *Juncus prismatocarpus*" (Juncaceae). Further, it is unlikely that the slender leaves of this *Juncus* could support a mature female larva of *S. imparella*, the adult of which has a wing span of nearly 5 cm. As other Australian species of the genus, especially the closely allied *S. helodes* and *S. percna*, have been taken in association with Cyperaceae, Meyrick's host record remains doubtful.

The males of *S. imparella* and related species usually have very dark forewings, and, unlike the *S. praelata* group, have the cornutus of the aedoeagus represented by 3 thorns and a slightly curved horn, instead of 2 thorns and a horn. In both sexes, *S. imparella* is usually much larger than *S. helodes* and *S. percna*. Of diagnostic value is the shape of the gnathos and uncus, while the scale-like projections and marginal serrations of the subteguminal processes of the male of *S. imparella* also distinguish it from these two species.

In the female of *S. imparella*, the underside of the wings is dark fuscous in the basal three-quarters. This at once distinguishes the species from *S. chrysorrhoa*, *S. limnochares*, and *S. percna*. The frenulum, which is a single stout bristle in *S. imparella*, also separates the species both from *S. chrysorrhoa* and *S. limnochares* in which 2 bristles are present. The dark fuscous costa and the light orange-yellow anal tuft distinguish *S. xantharrenes*, while the smaller size and white anal tuft separates the female of *S. helodes*. Specimens of *S. imparella* with the ochreous brown or fuscous forewings and pure white hindwings are large, distinctive insects and can be confused with no other Australian species.

SCIRPOPHAGA HELODES,* sp. nov.

Figs. 5*C*, 5*D*, 7*F*; Plate 1, Figs. 9 and 10

Types.—Holotype male (genitalia slide No. P121), 2 male and 4 female paratypes labelled "Dingo, Q., 19 Mar. 1958, I. F. B. Common, at rest on *Eleocharis dulcis*"; allotype female (genitalia slide No. P132), 1 male and 15 female paratypes labelled "12 mls. E. of Duaringa, Q., 18 Mar. 1958, I. F. B. Common"; 1 female paratype "15 mls. E. of Duaringa, Q., 4 Apr. 1957, I. F. B. Common"; 1 female paratype "Hedlow Ck., near Yeppoon, Q., 22 Mar. 1958, I. F. B. Common". Holotype male, allotype female, and 18 paratypes in the Division of Entomology Museum, C.S.I.R.O., Canberra. One male and one female paratype deposited in British Museum (Natural History), and one female paratype in each of the following museums: Queensland Museum, Brisbane; Australian Museum, Sydney; National Museum of Victoria, Melbourne; and South Australian Museum, Adelaide.

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* ἑλωδης, frequenting marshes.

Holotype male.—Head and antenna ochreous brown, labial palpus ochreous brown, suffused with fuscous on outer surface, in length 2·4 times diameter of eye. Thorax ochreous brown; anterior and middle legs ochreous brown, suffused with fuscous on outer surface, middle tarsi and posterior legs whitish. Abdomen ochreous white, suffused with ochreous brown on dorsum. Forewing ochreous brown, suffused with dark fuscous, especially on costa and on termen, markings indistinct, dark fuscous; an indistinct transverse fascia at one-third, 2 small spots at end of cell, at upper and lower angles, an oblique diffuse line from costa near apex to dorsum before tornus, indistinct dots on termen at end of veins; cilia fuscous in basal half, greyish apically. Hindwing white, suffused with fuscous towards termen, dark fuscous dots on margin at end of veins. Expanse 23·0 mm.

Allotype female.—Head, antenna, and palpi white, in length labial palpus twice diameter of eye. Thorax white, legs white, with some fuscous suffusion on outer surface and on bases of tarsal segments. Abdomen white, suffused with pale ochreous on dorsum, especially towards base, anal tuft pale ochreous white. Forewing and cilia white; underside white, suffused with fuscous in basal three-quarters, except on costa which is white. Hindwing and cilia white; underside white, slight fuscous suffusion on costa; frenulum a single stout bristle. Expanse 30·6 mm.

Male genitalia (*holotype*).—Uncus moderately tapered; gnathos arms uniting obliquely; subteguminal processes moderate, rounded, without obvious marginal serrations or scale-like projections on outer surface; aedoeagus with cornuti represented by 3 thorns and a slightly curved horn.

Female genitalia (*allotype*).—Ductus bursae expanded between junction of ductus seminalis and ostium, where the lining is more strongly sclerotized; corpus bursae spherical; anterior apophyses slender.

Expanse.—Male 20·9–24·2 mm, female 25·8–32·4 mm.

Specimens examined.—14 ♂♂, 37 ♀♀.

Distribution.—Central and southern Queensland. The author has examined specimens from the following localities: QUEENSLAND: 20 miles W. of Biggenden, Dingo, Duaringa, Esk, Gayndah, 25 miles N. of Gin Gin, Hedlow Creek (near Yeppoon,) Injune, Lake Clarendon, Roma, Rosewood.

Comments.—*S. helodes* clearly belongs to the *S. imparella* group of species. Of special importance is the presence of 3 thorns in the aedoeagus of the male and the rather differently formed lining of the ductus bursae in the female.

The male of *S. helodes* is usually much smaller than that of *S. imparella*, the arms of the gnathos are less abruptly united and the subteguminal processes lack the scale-like surface projections and distinct marginal serrations found in *S. imparella*. Compared with the male of *S. percna*, *S. helodes* is similar in size but with broader forewings. The uncus and gnathos are also much shorter, the arms of the gnathos unite much more abruptly, and the valva is not as broad.

In the female *S. helodes* is much smaller than *S. imparella* and usually rather smaller than *S. percna*. The upperside of both wings is pure, rather chalky white, not suffused with ochreous or fuscous as in *S. imparella*, or the shining very pale ochreous of the forewing of *S. percna*. The underside in *S. percna* also lacks the fuscous suffusion of both *S. helodes* and *S. imparella*.

As in *S. imparella*, the males are very variable in colour and markings. The forewings of some specimens are uniformly ochreous brown with little or no fuscous suffusion, and without markings; the markings in others may be more or less distinct and the ground colour may be uniform ochreous brown or suffused with dark fuscous. The hindwings sometimes have a fairly distinct oblique fuscous apical fascia in the outer third of the wing, on the inner margin of which there is a strong inward projection about the middle. The females appear to be extremely uniform in size and coloration.

Several females and an occasional male of *S. helodes* were observed resting on the stems of *Eleocharis dulcis* at Dingo, central Qld., along with both sexes of *S. xantharrenes* and *H. acentrus*. However, the species was not as common as either of the latter. Both sexes were again taken in close proximity to one another near Biggenden and at Esk, Qld., where they were resting on stems of *E. sphacelata*. A further female was taken at rest on this rush at Lake Clarendon. At these last three localities, this was the only species taken. There is no doubt therefore that the sexes are correctly associated. The larvae probably bore in the stems of *Eleocharis*.

SCIRPOPHAGA PERCNA,* sp. nov.

Figs. 5*E*, 5*F*, 7*G*; Plate 1, Fig. 11

Types.—Holotype male (genitalia slide No. P122) and 1 male paratype labelled "Darwin, N.T., G. F. Hill"; allotype female (genitalia slide No. P139) and 1 male paratype labelled "Darwin, N.T., 2 Apr. 1959, I. F. B. Common"; 1 male paratype "P. Darwin, March '09, F. P. Dodd"; 1 male paratype "P. Darwin, Dec. '08, F. P. Dodd"; 2 male paratypes "P. Darwin, Feb. '09" and "March '09". 1 male paratype "Humpty Doo, N.T., 24/8/56, L. D. Crawford"; 15 male and 13 female paratypes "Humpty Doo, N.T., 2–3 Apr. 1959, I. F. B. Common"; 1 male and 2 female paratypes with same label data but collected 6 Apr. 1959 "at rest on *Eleocharis dulcis*"; 9 male and 6 female paratypes "Humpty Doo, N.T., E. B. Boerema" collected in a light trap from January to March and in September 1959. Holotype, allotype, and 41 paratypes in the Division of Entomology Museum, C.S.I.R.O., Canberra; 1 male and 1 female paratype deposited in each of the following museums: British Museum (Natural History); Queensland Museum, Brisbane; Australian Museum, Sydney; National Museum of Victoria, Melbourne; and South Australian Museum, Adelaide. Two further male paratypes from the National Museum of Victoria collection, and one from the South Australian Museum.

Holotype male.—Head and antenna ochreous brown, labial palpus ochreous brown with slight fuscous suffusion on outer surface, in length 1·6 times diameter of eye. Prothorax and mesothorax ochreous, patagia and base of tegulae suffused with light fuscous, metathorax white; anterior and middle legs ochreous brown, suffused with fuscous on outer surface, middle tarsi and posterior legs white. Abdomen white. Forewing ochreous with slight fuscous suffusion, especially on costa towards base, markings dark fuscous; a transverse fascia at one-sixth not reaching dorsum; another at two-fifths not reaching dorsum and strongly angled outwards above middle; a small spot at upper angle of cell; an oblique fascia from costa just before apex to dorsum at four-fifths, less distinct towards dorsum, and with inner margin angled strongly inwards just above lower angle of cell; a series of dots on termen at end of veins; cilia ochreous. Hindwing white, suffused with fuscous in outer half, with indistinct dots on margin at end of veins. Expanse 22·4 mm.

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* *περκνος*, dark-coloured.

Allotype female.—Head white; antenna white at base, suffused with fuscous distally; labial palpus white, apical segment and outer surface of second segment suffused with fuscous, in length 1·7 times diameter of eye. Thorax white, legs white, anterior and middle legs suffused with fuscous. Abdomen shining white, dorsum with a few ochreous scales towards base, anal tuft ochreous white. Forewing very pale ochreous, shining, cilia white; underside of forewing dull ochreous white, of hindwing shining white. Hindwing and cilia shining white; underside shining white; frenulum a single stout bristle. Expanse 33·6 mm.

Male genitalia (*holotype*).—Uncus long, gently tapered; gnathos arms united obliquely, nearly as long as uncus; subteguminal processes moderate, rounded, with a few minute serrations on inner surface; aedoeagus with cornuti represented by 3 thorns and a slender horn with enlarged flattened base.

Female genitalia (*allotype*).—Ductus bursae nearly uniform in diameter, strongly bent at junction of ductus seminalis; corpus bursae oval; anterior apophyses slender.

Expanse.—Paratypic series: male 18·5–25·8 mm, female 26·1–38·8 mm.

Specimens examined.—49 ♂♂, 26 ♀♀.

Distribution.—Coastal northern Australia from Mackay, Qld., to Darwin, N.T. The author has examined specimens from the following localities: QUEENSLAND: Cairns, Mackay, Silver Plains (Cape York Peninsula), Townsville. NORTHERN TERRITORY: Darwin, Groote Eylandt, Humpty Doo, Marrakai.

Comments.—With *S. helodes*, *S. percna* belongs to the *S. imparella* species group. The strongly quadrate valva of the male genitalia, and the long tapering uncus and gnathos distinguish it from both *S. helodes* and *S. imparella*. The forewing is narrower in *S. percna* than in either of the other two, and the markings are usually more distinct, though again varying greatly in intensity.

In the female, the underside of the forewing of *S. percna* is not suffused with fuscous as in *S. helodes* and *S. imparella*, and the genitalia are quite distinct. Of special note is the uniform diameter of the ductus bursae, which is bent at an angle at the junction of the ductus seminalis.

Three specimens of *S. percna* were taken by the author at Humpty Doo, N.T., at rest on stems of *Eleocharis dulcis*, which will probably prove to be its host plant.

SCIRPOPHAGA OCHROLEUCA Meyrick

Fig. 7*H*; Plate 2, Fig. 2

Scirpophaga ochroleuca Meyrick, 1882, Proc. Linn. Soc. N.S.W. **7**: 162.

Types.—Meyrick's original two specimens in the British Museum (Natural History) are a male (without abdomen) and a female, not two males as stated by

Meyrick. Mr. D. S. Fletcher has kindly selected the female labelled "Coomooboolaroo, Queensland, GB/77", which is hereby designated as the lectotype.

Female genitalia.—Ductus seminalis joining ductus bursae at its junction with ostium; sclerotized lining present for a short distance within ductus bursae and continued for a short distance into ductus seminalis; corpus bursae without internal spining; outer part of ostium densely clothed with minute spines.

Expanse.—Female 22·1–28·8 mm.

Specimens examined.—8 ♀♀.

Distribution.—Central Queensland. In the Division of Entomology Museum, C.S.I.R.O., Canberra, there is a series of five females labelled "25 mls. N. of Gin Gin, Q., 23 Mar. 1958, I.F.B. Common" and one female labelled "Hedlow Ck., near Yeppoon, Q., 22 Mar. 1958, I.F.B. Common". All of these specimens were taken at light. The type specimens came from the property of the late George Barnard near Duaringa, central Qld.

Two female specimens from the Northern Territory, with genitalia very similar to those of *S. ochroleuca*, are in the Division of Entomology Museum, C.S.I.R.O. They are from Humpty Doo (E. B. Boerema) and the Daly R. (G. F. Hill). The species may therefore prove to have a wide distribution in coastal northern Australia.

Comments.—This species is clearly misplaced in *Scirpophaga* and probably also in the other known genera. However, it would seem unwise to erect a new genus for it until males are available for study.

From information supplied by Mr. D. S. Fletcher, the female of *Scirpophaga fusciflua* Hampson from Ceylon, which Hampson (1895) erroneously synonymized with *S. gilviberbis* Zeller, has genitalia very similar to *S. ochroleuca*, and is apparently congeneric with it. *S. gilviberbis*, on the other hand, should be referred to *Niphadoses* (new combination).

S. ochroleuca can be readily distinguished from the remainder of the known Australian species of Schoenobiinae by the position of the ductus seminalis and the extension into it of the sclerotized lining of the posterior portion of the ductus bursae. The labial palpus is slender and short, in length 1·5 times the diameter of the eye. The whole insect is white except for the forewing which is very slightly tinged with ochreous. In 4 of the 6 specimens examined, the veins Sc and R_1 of the forewing are anastomosed for a short distance. The frenulum in the female is a single stout bristle.

Genus HELONASTES,* gen. nov.

Type species *Helonastes acentrus*, sp. nov.

Proboscis short, weak; antenna in male finely serrate and ciliate, in female shorter, with short cilia; labial palpus (Fig. 2*D*) moderately long in both sexes, smooth-scaled, apical segment about half length of second, slightly tapering, porrected; maxillary palpi smooth-scaled, nearly half length of labial palpi. Forewing (Fig. 1*F*) moderately broad, apex broadly rounded; R_1 from three-quarters cell, curving towards Sc in middle, R_2 from near upper angle of cell, R_3 and R_4 stalked from near upper angle, R_5 from upper angle of cell, equidistant at base between R_{3+4} and M_1, M_2 and M_3 approximated but separate at base, M_3 from lower angle of cell, Cu_1 from near angle, Cu_2 from three-quarters cell. Hindwing (Fig. 1*F*) with *Rs* and M_1 connate or very short-stalked from upper angle, M_3 from lower angle of cell, Cu_2 from before two-thirds cell. Abdomen of male without differentiated flattened brush of scales on posterior margin of seventh sternite, their place being taken by rather more densely arranged normal scales readily removed during dissection, along with other body scales; eighth sternite with central membranous area and associated thickened areas of integument; abdomen of female with dense posterior tuft of deciduous hair-scales.

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* ἕλος, marsh; ναστης, inhabitant; masculine.

Male genitalia.—Uncus gradually tapering, with rounded apex; gnathos arms united in centre and drawn out to slender point, almost as long as uncus; tegumen with dorsal thickening in form of 2 subparallel thickened bands, and with a pair of rounded, strongly sclerotized processes beneath, projecting downwards; valva simple, with costa and dorsum nearly straight; anellus membranous, finely spined, surrounding aedoeagus; aedoeagus nearly straight, narrower apically, without cornuti, vesica with numerous minute rounded projections.

Female genitalia.—Ostium broad, membranous, densely clothed with minute spines on inner surface; ductus bursae narrowing towards junction of ductus seminalis, which is close to corpus bursae, between ductus seminalis and ostium with strong but incomplete sclerotization, U-shaped in cross section, with opening towards left side, between ductus seminalis and corpus bursae broad, sclerotized throughout; corpus bursae small, spherical, membranous, without signum, but lined with minute spines in anterior half.

As defined, the genus is monotypic. The single species, *H. acentrus*, though with some features similar to *Scirpophaga*, has several characters in both sexes which appear to justify generic separation. The greatest importance has been attached to the aberrant characters of the genitalia, by which it may be distinguished from other genera in the group. In the male, the modified thickening of the dorsum of the tegumen, and the absence of cornuti in the aedoeagus, separate the genus from *Scirpophaga* and other Australian genera. In the female, the form of the sclerotization of the ductus bursae, the position of the junction of the ductus seminalis, and the size and spining of the corpus bursae distinguish it from the other Australian genera. Though the differentiated ventral flap of modified scales on the seventh sternite is also lacking in the type species of *Niphadoses*, it is present in *N. hoplites*. However, it is strongly developed in the species of *Scirpophaga* examined by the author, and in all the other Australian species of the group with the exception of *Tipanaea patulella* Walk.

In addition to the characters of the genitalia and abdomen, the absence of any white on the female of *H. acentrus* is another character which differentiates the species from *Scirpophaga*.

Both sexes of *H. acentrus* were found commonly at rest on the stems of *Eleocharis dulcis*, associated with *Scirpophaga xantharrenes* and *S. helodes*, at Dingo, central Qld. This rush is therefore probably the host plant.

HELONASTES ACENTRUS,* sp. nov.

Figs. 1*F*, 2*D*, 5*G*, 5*H*, 8*A*; Plate 1, Figs. 12 and 13

Types.—Holotype male, allotype female (genitalia slides Nos. P119 and P130), 25 male and 25 female paratypes labelled "Dingo, Q., 19 Mar. 1958, I. F. B. Common, at rest on *Eleocharis dulcis*"; 2 male and 6 female paratypes labelled "12 mls. E. of Duaringa, Q., 18 Mar. 1958, I. F. B. Common"; 1 female paratype "15 mls. E. of Duaringa, Q., 4 Apr. 1957, I. F. B. Common".

Holotype, allotype, and 46 paratypes in the Division of Entomology Museum, C.S.I.R.O., Canberra; a pair of paratypes deposited in each of the following collections: British Museum (Natural History), Canadian National Collection, Ottawa; Queensland Museum, Brisbane; Australian Museum, Sydney; National Museum of Victoria, Melbourne; and South Australian Museum, Adelaide.

Holotype male.—Head, antenna, and palpi ochreous brown, labial palpus in length 2·3 times diameter of eye. Thorax ochreous brown; anterior legs with coxae and femora ochreous brown, tibiae and tarsi fuscous, middle and posterior legs pale ochreous. Abdomen pale ochreous, with some ochreous brown scales on dorsum of basal segments. Forewing with ground colour ochreous brown (buckthorn brown of Ridgway 1912), markings dark brown, a very indistinct transverse line at one-fifth, a second before one-half consisting primarily of 2 spots, one on fold and another beneath costa; a third indistinct oblique line from costa just before apex to dorsum before tornus, including a more distinct spot near dorsum; a small darker dot at end of cell; cilia ochreous, darker at base. Hindwing and cilia ochreous grey. Expanse 21·5 mm.

Allotype female.—Head, antenna, and palpi dull ochreous, labial palpus in length 2·0 times diameter of eye. Thorax ochreous brown; legs ochreous grey with some dark brown suffusion. Abdomen pale ochreous with some ochreous scales on dorsum towards base, anal tuft dull ochreous. Forewing pale ochreous, suffused with dark brown on costa and dorsum, markings dark brown; a transverse line at one-sixth, a second at two-fifths, with strong outward projection in middle; a dot at end of cell; an oblique line from costa at five-sixths to dorsum before tornus; cilia pale ochreous, hindwing and cilia grey, pale ochreous at apex; frenulum a single stout bristle. Expanse 30·3 mm.

Expanse.—Paratypic series, male 19·4–22·1 mm, female 28·2–35·4 mm.

Specimens examined.—29 ♂♂, 33 ♀♀.

Distribution.—Known only from Dingo and Duaringa, central Qld.

Comments.—The male of *H. acentrus* bears a superficial resemblance to the males of *S. helodes*, *S. percna*, and *S. imparella*, but is usually slightly smaller and may be distinguished by its ochreous brown coloration. The genitalia, as indicated under the generic description, provide several diagnostic characters.

The female can be distinguished readily from all other Australian species of the group by its dull ochreous to ochreous brown colour. In some specimens, including the allotype, the forewings bear a distinctive pattern, but in many the markings are absent.

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* *ἀκεντρος*, without thorns.

Genus NIPHADOSES,* gen. nov.

Type species *Niphadoses palleucus*, sp. nov.

Proboscis short, weak; antenna in male finely serrate and ciliate, in female much shorter, with short cilia; frons with scales long, projecting partly over maxillary palpi; labial palpus (Fig. 2*C*) long in both sexes, apical segment porrected, less than one-third length of second; usually with expanded scales above and beneath, maxillary palpi with expanded scales. Forewing (Fig. 1*C*) with R_1 from two-thirds or three-quarters of cell, usually anastomosing with *Sc* for at least part of its length, occasionally free, R_2 from before upper angle of cell, R_3 and R_4 stalked from upper angle, R_4 to apex, R_5 separate to termen, M_1 closer to R_5 than to M_2, M_2 from near M_3, M_3 from lower angle of cell, Cu_1 from well before angle, Cu_2 from before three-quarters of cell. Hindwing (Fig. 1*C*) with *Rs* and M_1 approximated from upper angle of cell, M_2 and M_3 approximated at base, M_3 from lower angle, Cu_1 from well before angle, Cu_2 from before two-thirds of cell. Abdomen of male without or sometimes with, differentiated flattened brush of scales on posterior margin of seventh sternite; eighth with central membranous area and associated thickened areas of integument; abdomen of female with dense posterior tuft of deciduous hair-scales.

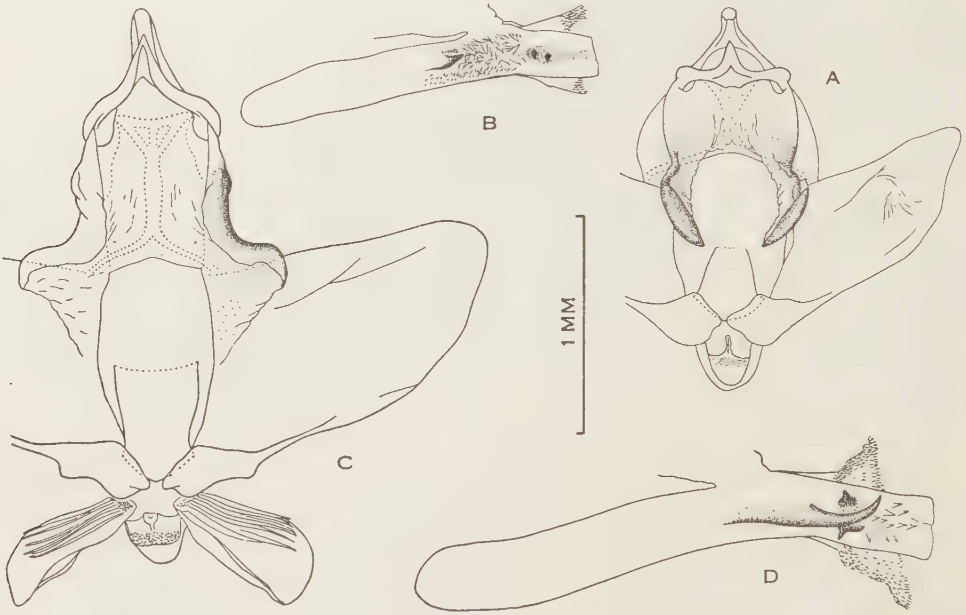

Fig. 6.—Male genitalia of: *A*, *B*, *Niphadoses palleucus*, sp. nov., holotype, 25 miles N. of Gin Gin, Qld.; *C*, *D*, *N. hoplites*, sp. nov., holotype, 25 miles N. of Gin Gin, Qld.

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* νιφαδος, snowflake; σης, moth; masculine.

Male genitalia.—Uncus short; gnathos arms united in centre abruptly or rather obliquely, and drawn out to a short acute point; tegumen broad, with dorsal thickening X-shaped, and with a pair of rounded, strongly sclerotized processes beneath, projecting downwards; valva simple, with costa straight or slightly concave, dorsum convex, apex rounded; anellus membranous, finely spined, surrounding aedoeagus; aedoeagus nearly straight, cornuti represented by a pair of thorns, an elongate curved horn, and numerous short acute spines.

Female genitalia.—Ostium membranous, clothed with minute spines on inner surface; ductus bursae of nearly uniform diameter, or greatly expanded between junction of ductus seminalis and corpus bursae, with a strongly sclerotized lining between ductus seminalis and ostium, junction of ductus seminalis closer to ostium than to corpus bursae; corpus bursae spherical, without signum, densely lined with minute spines throughout.

The genus as defined above is erected to include the type species, two other Australian species *N. hoplites* and *N. elachia*, *N. chionotus* (Meyr.) (new combination) from New Guinea, and the Indian species *N. gilbiverbis* (Zell.) (new combination), originally described in the genus *Scirpophaga.*

From the other Australian genera, *Niphadoses* may be readily recognized by the long labial palpi in both sexes, with their spreading scales above and beneath and the anastomoses of veins R_1 and *Sc* in the forewing. In occasional specimens, these veins are separate. The long scales of the tegulae of the thorax are capable of being greatly expanded, giving the thorax a ruffled appearance, while the cilia on the margins of the wings are also long. The short uncus and gnathos, the relatively broad tegumen and the shape of the dorsal thickening of the tegumen are also characteristic. This X-shaped thickening varies considerably from one specimen to another, but the general shape persists. The female genitalia are rather similar to those of the *imparella* group of *Scirpophaga*, but the minute spining of the ostium is much sparser and the characters of the palpi, venation, and general facies serve to distinguish them readily.

The labial palpi in both sexes of *Niphadoses* are long, as in *Schoenobius*, but the genitalia are quite distinct. The long, gradually tapered uncus and gnathos in the latter, the reduced subteguminal processes, the roughly triangular dorsum of the tegumen, the cornuti in the form of a single curved thorn and the shape of the valva, readily distinguish the males. In the female of *Schoenobius*, distinguishing characters include the scattered spining of the ostium, the complete absence of minute spines in the oval membranous corpus bursae, and the slightly sclerotized ductus bursae in the region of the ductus seminalis which joins the ductus bursae near the ostium.

The host plants of the species of *Niphadoses* are not known with any degree of certainty, but it is probable that they bore in the stems of Gramineae. At the C.S.I.R.O. Kimberley Research Station, north-western Australia, this species is often present along with *Tryporyza innotata* in very large numbers amongst experimental rice crops. Mr. A. L. Chapman (personal communication) has reared a specimen from a pupa collected at the base of a rice plant, suggesting that the species does attack this crop.

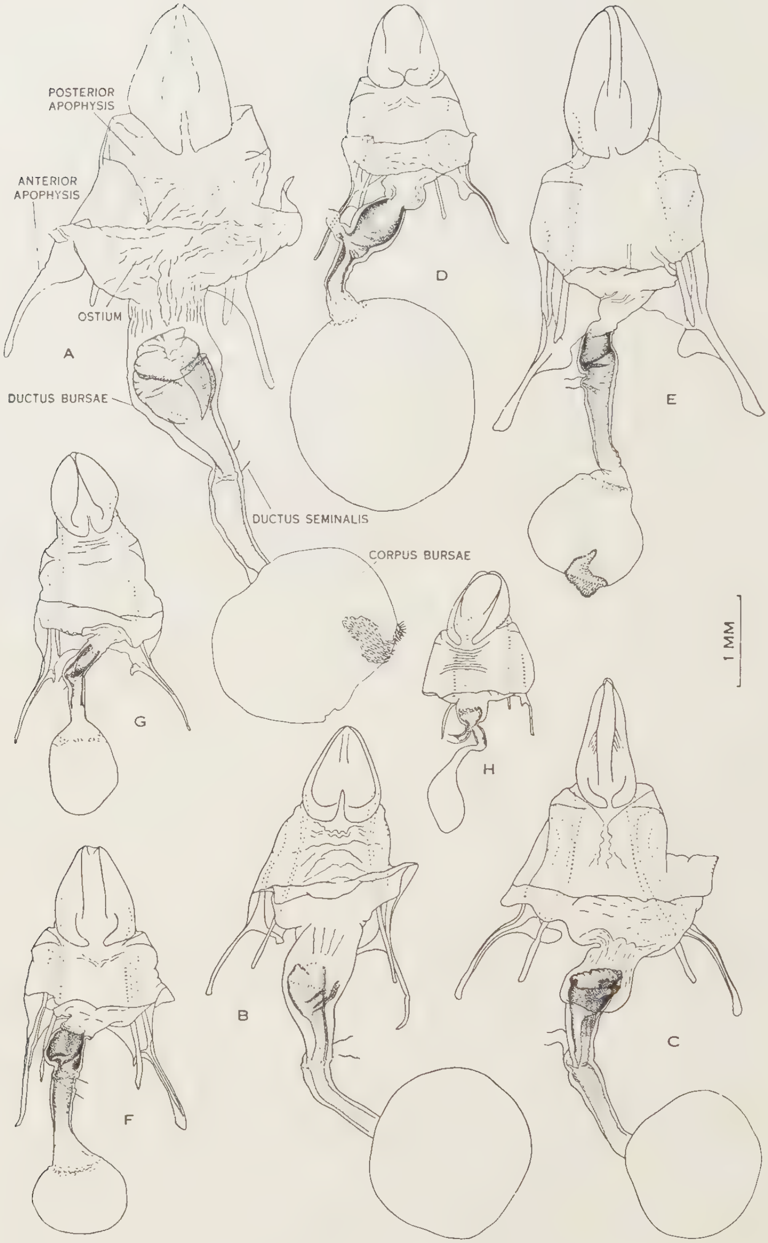

Fig. 7.—Female genitalia of: *A*, *Scirpophaga praelata* Scop., Macedonia; *B*, *S. chrysorrhoa* Zell., Burringbar, N.S.W.; *C*, *S. limnochares*, sp. nov., allotype, Coraki, N.S.W.; *D*, *S. xantharrenes*, sp. nov., allotype, 12 miles E. of Duaringa, Qld.; *E*, *S. imparella* (Meyr.), Colo R., N.S.W.; *F*, *S. helodes*, sp. nov., allotype, 12 miles E. of Duaringa, Qld.; *G*, *S. percna*, sp. nov., allotype, Darwin; *H*, *S. ochroleuca* Meyr., 25 miles N. of Gin Gin, Qld.

Specimens of the two further species of *Niphadoses*, one from Humpty Doo, N.T., and the other from Silver Plains, Cape York Peninsula, Qld. (J. L. Wassell), are in the Division of Entomology Museum, C.S.I.R.O., Canberra. One of these may prove to be *N. chionotus*, but their positive determination awaits the collection of further specimens of *N. chionotus*, particularly females.

Key to Australian Species of the Genus Niphadoses

1. Cornuti in male aedoeagus dominated by a very long, strongly curved horn; ductus bursae of female very broad between ductus seminalis and corpus bursae . . *N. hoplites*, sp. nov.
   Cornuti in male aedoeagus small without dominant horn; ductus bursae of female more or less uniform in diameter 2

2(1). Ductus bursae of female bent at junction of ductus seminalis, with strongly sclerotized lining throughout most of its length . . . . *N. palleucus*, sp. nov.
   Ductus bursae of female almost straight, with lightly sclerotized lining, mainly between ostium and junction of ductus seminalis . . . . *N. elachia*, sp. nov.

Niphadoses palleucus,* sp. nov.

Figs. 1*C*, 2*C*, 6*A*, 6*B*, 8*C*; Plate 2, Figs. 10 and 11

Types.—Holotype male, allotype female (genitalia slides Nos. P117 and P128), 10 male and 11 female paratypes labelled "25 mls. N. of Gin Gin, Q., 23 Mar. 1958, I. F. B. Common"; 29 male and 27 female paratypes "Hedlow Creek, near Yeppoon, Q., 22 Mar. 1958, I. F. B. Common". Holotype, allotype, and 53 paratypes in the Division of Entomology Museum, C.S.I.R.O., Canberra; two pairs of paratypes deposited in each of the following collections: British Museum (Natural History); Canadian National Collection, Ottawa; Queensland Museum, Brisbane; Australian Museum, Sydney; National Museum of Victoria, Melbourne; and South Australian Museum, Adelaide.

Holotype male.—Head, antenna, and palpi white, length of labial palpus 3·7 times diameter of eye. Thorax white; legs white, anterior and middle legs suffused with fuscous. Abdomen white, dorsum suffused with ochreous. Forewing and cilia white, with very slight ochreous white suffusion, especially along costa; underside with slight fuscous suffusion, especially along costa; R_1 anastomosing with *Sc*. Hindwing and cilia white; underside white. Expanse 21·8 mm.

Allotype female.—Similar to male, but without fuscous suffusion beneath forewing; abdomen white, suffused with pale ochreous, dorsum of basal three segments ochreous, anal tuft ochreous white. Frenulum a single stout bristle. Expanse 22·7 mm.

Male genitalia (*holotype*).—Gnathos arms uniting abruptly in middle and produced to a short acute point; juxta constricted above; aedoeagus with cornuti represented by a short curved horn, 2 small thorns, and a large series of small acute spines.

Female genitalia (*allotype*).—Ductus bursae of almost uniform diameter, usually strongly bent at junction of ductus seminalis, with strongly sclerotized lining throughout.

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* παλλευκος, all white.

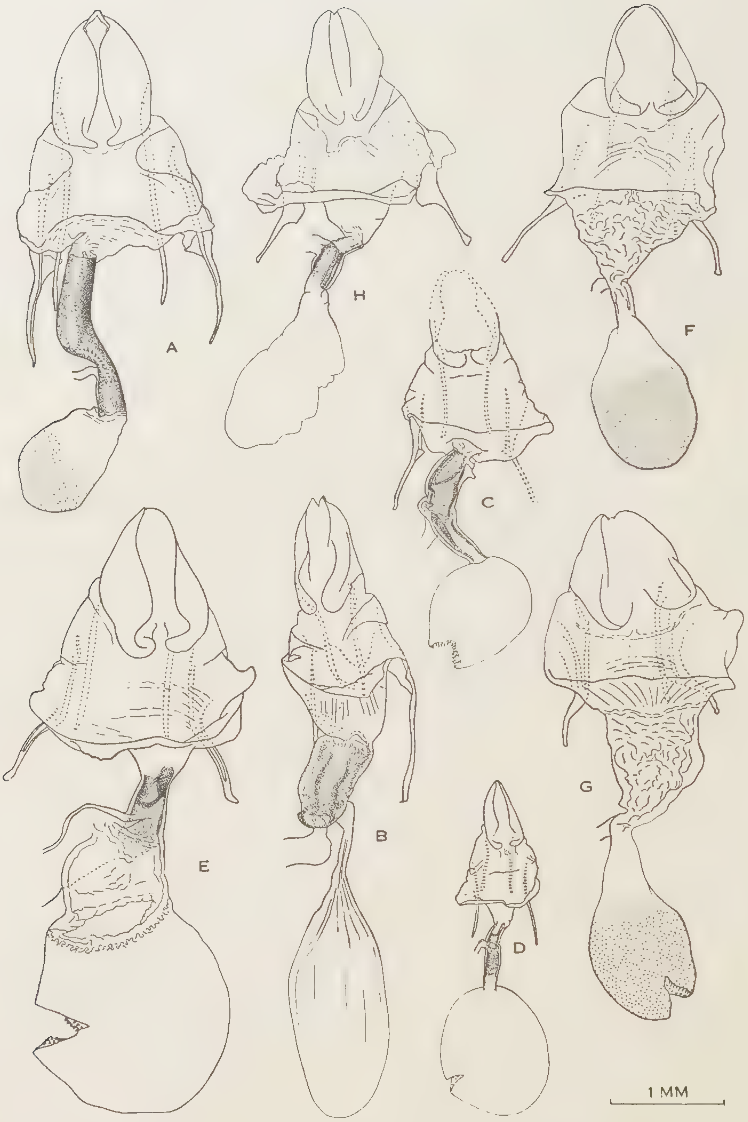

Fig. 8.—Female genitalia of: *A*, *Helonastes acentrus*, sp. nov., allotype, Dingo, Qld.; *B*, *Catagela adoceta*, sp. nov., allotype, 25 miles N. of Gin Gin, Qld.; *C*, *Niphadoses palleucus*, sp. nov., allotype 25 miles N. of Gin Gin, Qld.; *D*, *N. elachia*, sp. nov., holotype, Hedlow Creek, near Yeppoon, Qld.; *E*, *N. hoplites*, sp. nov., allotype, 25 miles N. of Gin Gin, Qld.; *F*, *Tryporyza innotata* (Walk.), Ivanhoe, north-western Australia; *G*, *T. melanostigma* (Turn.), paratype, Claudie R., Qld.; *H*, *Tipanaea patulella* Walk., Brisbane.

Expanse.—Paratypic series: male 17·0–23·6 mm, female 19·7–26·0 mm.

Specimens examined.—68 ♂♂, 90 ♀♀.

Distribution.—Known from central and south-eastern Queensland, and from north-western Australia. Specimens from the following localities have been examined by the author: QUEENSLAND: 12 miles E. of Duaringa, 25 miles N. of Gin Gin, 18 miles S. of Gympie, Hedlow Creek (near Yeppoon), Rockhampton. WESTERN AUSTRALIA: Ivanhoe (near Wyndham).

Comments.—From *N. hoplites*, the species can be readily recognized by the cornuti of the male aedoeagus and the form of the ductus bursae of the female genitalia. The labial palpi are also longer in both sexes than in *N. hoplites*. From *N. elachia*, in which only females are known, the form of the thickened lining of the ductus bursae in the female genitalia is the most reliable character. *N. palleucus* is also much larger than *N. elachia*.

The long series of specimens of *N. palleucus* available to the author shows variation in the width of the wings. In the holotype, allotype, and several paratypes from the type locality both forewing and hindwing are relatively narrow. Some of the paratypes from Hedlow Creek and specimens from Duaringa and other localities are, on the whole, broader-winged, though intermediates occur. The degree of roughening of the scales of the palpi and the extent to which the long scales of the tegulae of the thorax are expanded are also variable. Slight differences, apparently not correlated with these superficial differences, were observed in the male genitalia, particularly in the length of the aedoeagus. Specimens from Ivanhoe, near Wyndham, are more closely similar to the narrow-winged specimens from the type locality. There seems to be no alternative therefore to the conclusion that the whole series of specimens belong to the one rather variable species. The condition of R_1 of the forewing is also somewhat variable: in most specimens R_1 anastomoses with *Sc* from near its base, but in some it anastomoses for only part of its length, the two veins separating near the margin, while in an occasional specimen, R_1 is free throughout.

All the specimens from central and south-eastern Queensland were taken at light. At Ivanhoe, the species at times occurs very commonly in experimental rice crops and, as a specimen has been reared from a pupa taken at the base of a rice plant, it is suspected that it may contribute to the damage largely attributed to *Tryporyza innotata*.

NIPHADOSES ELACHIA,* sp. nov.

Fig. 8*E*; Plate 2, Fig. 12

Types.—Holotype female (genitalia slide No. P129) and 9 female paratypes labelled "Hedlow Creek, near Yeppoon, Q., 22 Mar. 1958, I. F. B. Common". Holotype and 5 paratypes in the Division of Entomology Museum, C.S.I.R.O., Canberra; 1 paratype deposited in each of the following collections: British Museum (Natural History); Australian Museum, Sydney; National Museum of Victoria, Melbourne; and South Australian Museum, Adelaide.

Holotype female.—Head, antenna, and palpi white, length of labial palpus 4·5 times diameter of eye. Thorax pale ochreous white; legs white, anterior legs suffused with light fuscous. Abdomen white, dorsum ochreous, tuft ochreous white. Forewing and cilia very pale ochreous white; underside white; R_1 anastomosing with *Sc*. Hindwing and cilia white; underside white; frenulum a single stout bristle. Expanse 14·5 mm.

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* ἐλαχεια, small.

Female genitalia (*holotype*).—Ductus bursae almost straight and of nearly uniform diameter, with lightly sclerotized lining mainly between ostium and junction of ductus seminalis.

Expanse.—Paratypic series: female 13·6–15·8 mm.

Specimens examined.—10 ♀♀.

Distribution.—Known only from central Queensland.

Comments.—The smallest species of the group in Australia, it has been taken only at the type locality in central Queensland. The type series of females only was taken at light. Its host plant is not known.

It is readily distinguished from *N. hoplites* by its small size, the pale ochreous white forewings, and the much longer labial palpi. In worn specimens, however, the pale ochreous colour of the forewings may be lost and they then appear white. The female genitalia also clearly separate these two species. *N. elachia* is not unlike a small, narrow-winged specimen of *N. palleucus*, but the sclerotization of the ductus bursae of the female genitalia, the length of the labial palpi, and the colour of the forewing serve to separate the two species.

NIPHADOSES HOPLITES,* sp. nov.

Figs. 6*C*, 6*D*, 8*E*; Plate 2, Figs. 13 and 14

Types.—Holotype male, allotype female (genitalia slides Nos. P120 and P127), 4 male and 14 female paratypes labelled "25 mls. N. of Gin Gin, Q., 23 Mar. 1958, I. F. B. Common"; 2 male and 5 female paratypes "12 mls. E. of Duaringa, Q., 18–21 Mar. 1958, I. F. B. Common". Holotype, allotype, and 18 paratypes in the Division of Entomology Museum, C.S.I.R.O., Canberra; 7 paratypes distributed as follows: 1 pair each in British Museum (Natural History) and South Australian Museum, Adelaide; 1 female each in Queensland Museum, Brisbane, Australian Museum, Sydney, and National Museum of Victoria, Melbourne.

Holotype male.—Head, antenna, and palpi white, palpi slightly suffused with fuscous near base, length of labial palpus 3·0 times diameter of eye. Thorax white, scales of tegulae greatly expanded over thorax; legs white, anterior and middle legs suffused with fuscous. Abdomen white, suffused with ochreous on dorsum, especially towards base. Forewing and cilia white, costal edge suffused with fuscous; underside white, suffused with fuscous, especially along costa; R_1 anastomosing with *Sc*. Hindwing and cilia white; underside white, with slight fuscous suffusion on costa. Expanse 26·4 mm.

Allotype female.—Similar to male but without fuscous suffusion on costa and underside of wings; anal tuft ochreous white. Frenulum a single stout bristle. Expanse 34·0 mm.

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* ὁπλιτης, heavily armed.

Male genitalia (*holotype*).—Gnathos arms uniting obliquely and produced to short acute point; juxta expanded above; aedoeagus with cornuti represented by a very large curved horn, 2 short thorns, and a series of small acute spines.

Female genitalia (*allotype*).—Ductus bursae between junction of ductus seminalis and corpus bursae greatly expanded, about half diameter of corpus bursae.

Expanse.—Paratypic series: male 25·8–29·4 mm, female 24·5–34·2 mm.

Specimens examined.—8 ♂♂, 21 ♀♀.

Distribution.—Central and south-eastern Queensland. Apart from the type locality specimens have been taken near Duaringa and 18 miles south of Gympie.

Comments.—This is the largest of the three Australian species of *Niphadoses.* In both sexes, the labial palpi are shorter than in *N. palleucus* and *N. elachia.* The cornuti of the male aedoeagus and the ductus bursae of the female genitalia immediately separate it from the other two species.

All the specimens of *N. hoplites* were taken at light and there is therefore no information about possible host plants.

Genus CATAGELA Walker

Catagela Walker, 1863, List Lep. Ins. Coll. Brit. Mus. **27**: 191.

Type species *Catagela adjurella* Walker, from Ceylon (by monotypy, since the only other species, *admotella* Walker, was only doubtfully included in *Catagela* by its author).

Proboscis short, weak; antenna in male finely serrate and ciliate, antenna in female shorter, with short cilia; labial palpus (Fig. 2*E*) long in both sexes, smooth-scaled, with fringe of long scales beneath, apical segment about half length of second, tapering, porrected; maxillary palpi smooth-scaled, about one-third length of labial palpi. Forewing (Fig. 1*E*) elongate, narrow, R_1 arising between two-thirds and three-quarters cell, not closely approximated to *Sc*, R_2 from near upper angle of cell, R_3 and R_4 stalked from near upper angle, R_4 to costa near apex, stem of R_{3+4} not closely approximated to R_2; R_5 from upper angle of cell, equidistant at base from R_{3+4} and M_1, M_2 and M_3 approximated but separate at base, M_3 from lower angle of cell, Cu_1 from before angle and Cu_2 from three-quarters cell. Hindwing (Fig. 1*E*) with *Rs* and M_1 connate from upper angle of cell, *Rs* anastomosing with $Sc-R_1$ for one-third its length, M_2 and M_3 approximated at base, M_3 from lower angle of cell, Cu_1 from near angle, Cu_2 from before two-thirds cell. Abdomen of male with flattened brush of scales on posterior margin of seventh sternite, projecting over eighth sternite; posterior margin of eighth sternite with median notch; abdomen of female with large and dense posterior tuft of deciduous hair-scales.

Male genitalia.—Uncus slender with rounded apex; gnathos arms uniting obliquely in centre and drawn out to a slender point, almost as long as uncus; tegumen with dorsal, Y-shaped thickening (Fig. 3*C*), and a pair of large, sclerotized processes beneath, projecting downwards on either side of aedoeagus; valva simple, curved, truncate, slightly tapered (distorted in genitalia slide of holotype of *C. adjurella*); juxta produced above into a long, slender, tapering sclerotized projection;

anellus a finely spined membrane surrounding the aedoeagus; aedoeagus nearly straight, cornutus a large curved, tapering spine.

Female genitalia.—Ostium broad, membranous, densely clothed with fine spines on inner surface, extended into entrance of ductus bursae; ductus bursae broadly expanded between ostium and junction of ductus seminalis, heavily sclerotized within, remainder of ductus bursae membranous; corpus bursae elongate, membranous, without signum, and without minute spines.

The most outstanding features of the genus *Catagela* are provided by the male genitalia. Here the juxta is produced above to form a long, heavily sclerotized process with tapering point, and the cornutus of the aedoeagus is in the form of a single large curved horn. In addition, the inverted Y-shaped thickening of the tegumen, with its short stem and long arms, is distinctive. The wings are narrow and pointed and the smooth-scaled labial palpi are long in both sexes.

The genitalia in the female are not likely to be confused with other Australian species. The membranous corpus bursae, without minute spines on its inner surface is also found only in *Tipanaea* and in *Scirpophaga ochroleuca*. However, both of these are white species, not likely to be confused. The female genitalia are also suggestive of *Schoenobius*, but in that genus the ductus seminalis leaves the ductus bursae in the middle of the sclerotized portion, whereas in *Catagela* it leaves at the anterior end. The male genitalia of these two genera are also very distinct.

CATAGELA ADOCETA,* sp. nov.

Figs. 1*E*, 2*E*, 3*C*, 3*D*, 8*B*; Plate 2, Figs. 4 and 5

Types.—Holotype male (genitalia slide No. P118) and 2 paratype males labelled "25 mls. N. of Gin Gin, Q., 16 Mar. 1958, I. F. B. Common"; allotype female with same label data but collected 23 Mar. 1958 (genitalia slide No. P131); 2 female paratypes "Hedlow Creek, near Yeppoon, Q., 22 Mar. 1958, I. F. B. Common" and 1 female paratype "12 mls. E. of Duaringa, Q., 18 Mar. 1958, I. F. B. Common". Holotype, allotype, and 3 paratypes in the Division of Entomology Museum, C.S.I.R.O., Canberra; a pair of paratypes deposited in British Museum (Natural History) and a female paratype in South Australian Museum, Adelaide.

Holotype male.—Head, antenna, and palpi orange-brown, length of labial palpus 3·2 times diameter of eye. Thorax orange-brown; legs pale ochreous, anterior legs suffused with grey. Abdomen pale ochreous, with some ochreous scaling on dorsum. Forewing shining ochreous, suffused with ferruginous and fuscous, especially on costal half of wing; a broad dark fuscous longitudinal streak above middle of wing from one-third to two-thirds wing, then dividing into 3 slender streaks along veins towards termen; an oblique fuscous line from apex to two-thirds dorsum; 2 round fuscous spots on fold, one at one-third and another just beyond one-half; a round dark orange-brown spot in cell beyond two-fifths and another at end of cell; a series of fuscous terminal dots on veins; cilia ferruginous with pinkish suffusion. Hindwing white, suffused with pale ochreous grey distally and with a few indistinct dark brown terminal dots on veins below apex. Expanse 23·9 mm.

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* ἀδοκητος, unexpected.

Allotype female.—Similar to male, but without terminal dots on hindwing; anal tuft pale ochreous. Frenulum a single stout bristle. Expanse 30·6 mm.

Male genitalia (*holotype*).—Subteguminal processes triangular in shape with curved apex; aedoeagus cylindrical.

Female genitalia (*allotype*).—See under generic description.

Expanse.—Paratypic series: male 23·9–25·2 mm, female 27·3–30·6 mm.

Specimens examined.—3 ♂♂, 11 ♀♀.

Distribution.—Queensland and the Northern Territory. Evidently the species is widely distributed in northern Australia. Apart from the type series, the author has examined specimens in the Division of Entomology Museum, C.S.I.R.O., Canberra, from the following localities: Silver Plains, Cape York Peninsula (J. L. Wassell), Brock's Creek (T. G. Campbell) and Humpty Doo, N.T.

Comments.—The Australian species, with its shining ferruginous forewings and whitish hindwings in both sexes, is a distinctive insect not likely to be confused with other species. The uncus and gnathos of the male genitalia are longer than in the holotype of *C. adjurella*, the type species, and the subteguminal processes are quite different in shape.

The single female of *C. adoceta* from Brock's Creek bears a label "*Schoenobius* n.sp.?, Det. A. J. Turner, 1931". As the type series was taken at light, there is no indication of the larval host plant.

Genus TRYPORYZA,* gen. nov.

Type species *Tipanaea innotata* Walker.

Proboscis short, weak; antenna in male finely serrate and ciliate, in female shorter, with short cilia; frons with projecting scales; labial palpus (Fig. 2*B*) long in both sexes, apical segment porrected, more than one-half length of second; scales only slightly expanded above on second segment. Forewing (Fig. 1*D*) with R_1 from before three-quarters cell, curved towards *Sc* in middle, R_2 from before upper angle of cell, R_3 and R_4 stalked from upper angle, R_4 to apex, R_5 separate to termen, M_1 closer to R_5 than to M_2, M_2 from near M_3, M_3 from lower angle of cell, Cu_1 from before angle, Cu_2 from before three-quarters cell. Hindwing (Fig. 1*D*) with *Rs* and M_1 approximated from upper angle of cell, M_2 from near M_3, M_3 from lower angle, Cu_1 from before angle, Cu_2 from just beyond one-half cell. Abdomen of male with a strong flattened brush of scales on posterior margin of seventh sternite; eighth sternite with central membranous area and associated thickened areas of integument; abdomen of female with dense posterior tuft of deciduous hair-scales.

Male genitalia.—Uncus long and tapering; gnathos arms united in centre and drawn out to a long point, nearly as long as uncus; tegumen broad, with indeterminate dorsal thickening, and with a pair of strong subteguminal processes in the form of heavily sclerotized single or bifid hooks, projecting downwards and backwards; valva simple; anellus membranous, finely spined, surrounding aedoeagus; aedoeagus nearly straight, cornuti represented by a pair of straight sclerotized horns directed towards orifice, or cornuti absent.

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* τρυπη, a boring; αρυζα, rice; feminine.

Female genitalia.—Ostium broad, not noticeably sclerotized, but thickened and strongly wrinkled, tapering to junction of ductus seminalis; ductus bursae short, expanding gradually into ovate corpus bursae, which is moderately lined with minute spines in anterior three-quarters, without signum.

The genus is erected to include *Scirpophaga butyrota* Meyrick from New Guinea and *Chilo incertulas* Walker, as well as the type species. The last two are of considerable economic importance as stem borers of cultivated rice and are known in the economic literature as *Schoenobius incertulas* and *Scirpophaga innotata* respectively. In addition, the Australian species *Schoenobius melanostigmus* Turner is referred tentatively to this genus.

The logical association of these species in a single genus is indicated by the genitalia, especially of the female. In the male the curved hook-like subteguminal processes are distinctive, while in the female the broad, thickened, and strongly wrinkled ostium is diagnostic.

It is probable that the stem-boring larvae are restricted to the Gramineae and possibly to the genus *Oryza*.

KEY TO AUSTRALIAN SPECIES OF THE GENUS TRYPORYZA

Females

Labial palpus of moderate length, less than 3 times diameter of eye, with appressed scales; frenulum with 2 bristles .... *T. innotata* (Walk.)

Labial palpus long, 4 times diameter of eye, with expanded scales; frenulum with 1 bristle .... *T. melanostigma* (Turn.)

TRYPORYZA INNOTATA (Walker)

Figs. 1*D*, 2*B*, 3*E*, 3*F*, 8*F*; Plate 2, Figs. 6 and 7

Tipanaea innotata Walker, 1863, List Lep. Ins. Coll. Brit. Mus. **28**: 523.

Type.—Walker's original description was based on a unique female labelled "Sarawak, Saunders Coll. 94–68" and "SAR", not a male as stated. Mr. D. S. Fletcher states that these labels are in Walker's handwriting. The holotype is in the British Museum (Natural History) (genitalia slide No. Pyralidae 4029).

Male.—Head, antenna, and palpi white, palpi suffused with fuscous on outer surface especially towards base, labial palpus about 2·3 times diameter of eye. Thorax white, base of tegulae sometimes with slight light fuscous suffusion; anterior legs fuscous, middle and posterior legs white, middle legs suffused with fuscous. Abdomen dull ochreous white, basal segment with ochreous dorsal suffusion. Forewing and cilia dull ochreous white, sometimes suffused with ochreous brown, especially along the veins, costa narrowly dark fuscous, especially in basal half; underside strongly suffused with fuscous. Hindwing and cilia shining white; underside white, suffused with fuscous, especially apically and towards costa.

Female.—Head, antenna, and palpi white, labial palpus about 2·7 times diameter of eye. Thorax dull white or ochreous white; legs dull white, anterior pair slightly suffused with light fuscous. Abdomen dull white, basal segment with slight ochreous dorsal suffusion, anal tuft dull ochreous white externally, covering a mass of ochreous brown hair-scales within. Forewing and cilia dull white or ochreous white; underside similar. Hindwing and cilia shining white; underside white; frenulum a pair of closely appressed bristles.

Male genitalia.—Subteguminal processes a pair of strong, single, smooth tapering hooks; aedoeagus with cornuti a pair of straight horns arising from a flattened, slightly curved base.

Female genitalia.—See generic description.

Expanse.—Male 20·6–27·3 mm, female 24·2–33·3 mm.

Specimens examined.—75♂♂, 59 ♀♀.

Distribution.—The species is probably widely distributed in Indonesia and northern Australia. Specimens from Java as well as from the following localities have been examined critically by the author: QUEENSLAND: Silver Plains, Cape York Peninsula (J. L. Wassell). NORTHERN TERRITORY: Humpty Doo, Sixty-mile. WESTERN AUSTRALIA: Ivanhoe.

Comments.—As the female genitalia of species in this genus do not provide the most reliable diagnostic specific characters, the specific identity of specimens from Java and northern Australia needs to be confirmed by the examination of further specimens of *T. innotata*, especially males, from Sarawak. The female holotype is the only specimen so far available from that locality. Efforts to have further specimens collected at Sarawak have been made on behalf of the author by Mr. T. Harrisson, Curator of the Sarawak Museum, but they have so far proved unsuccessful. The identity of rice stem borers from other areas of south-east Asia referred to this species needs to be checked critically.

The genitalia provide diagnostic characters for the separation of *T. innotata* from all other Australian species. In particular, the conspicuous hook-like teguminal processes in the male and the curiously thickened but unsclerotized ostium of the female are of special value. However, for field identification and where large numbers of specimens taken in light traps need to be determined in the course of ecological studies in northern Australia, various reliable superficial characters are available.

Of the species occurring in northern Australian rice areas, those most likely to be confused superficially with *T. innotata* are the species of *Scirpophaga* and *Niphadoses*. Only one Australian species of *Scirpophaga*, *S. phaedima*, is known to have a white male. From it the male of *T. innotata* can be distinguished by the length of the labial palpi which are relatively short (less than twice the diameter of the eye) in *S. phaedima* and relatively long (more than twice the diameter of the eye) in *T. innotata*. In addition, the forewing of the latter is a dull white, while in the former it is shining. Four species of *Scirpophaga* from northern Australia, *S. chrysorrhoa*, *S. xantharrenes*, *S. percna*, and *S. ochroleuca* have white females; the female of *S. phaedima* is not known but is probably also white. The labial palpi of the female of *T. innotata* is considerably longer (nearly three times diameter of eye) than in any of the species of *Scirpophaga*. The dull ochreous white forewings and the dull white abdomen in *T. innotata*, will also distinguish it from the species of *Scirpophaga*. The dull whitish anal tuft covering the inner ochreous brown hair scales in *T. innotata* is distinctive. The labial palpi are also useful for separating *T. innotata* from those species of *Niphadoses* known to occur in northern Australia. In the latter the palpi are very long, from three to five times the diameter of the eye, and are clothed with long and usually expanded scales above and beneath (compare Figs. 2*B* and 2*C*).

The eggs of *T. innotata* are deposited in batches, covered by the ochreous brown inner hair scales from the female anal tuft. These egg batches are usually found on the leaf blades of the rice host plant. Larvae tunnel in the crown or enter the internodes of the stem usually beneath the leaf sheath. The developing larva excavates the nodes and the interior layers of the wall of the hollow internode, usually making one or more circular, horizontal grooves deep enough to weaken the stem and to interfere with translocation in the plant. The resulting death of the growing shoot and associated leaves, or of the flower head, provides conspicuous evidence of the presence of one or more of the stem-boring larvae. Pupation occurs in a silken cocoon within the affected internode, the larva first having made a circular emergence hole to which it attaches the end of the cocoon. Larvae which develop late in the cropping season usually remain during the following dry season as prepupae within the crop stubble. Pupation and subsequent adult emergence apparently follows the first rains of the wet season.

In Java, *T. innotata* has been reared only from cultivated rice (Van der Goot 1925, Van der Laan 1959), but at the C.S.I.R.O. Kimberley Research Station, near Ivanhoe, north-western Australia, Mr. A. L. Chapman and Mr. E. C. B. Langfield have also reared the species from wild rice, *Oryza australiensis*. As botanists believe that wild rices were well established in Australia before European settlement (N. T. Burbidge, personal communication), there is no reason to suppose that *T. innotata* is not of natural occurrence in northern Australia. This conclusion is strengthened by Mr. J. L. Wassell's recent discovery of *T. innotata* at Silver Plains on the east coast of the Cape York Peninsula.

TRYPORYZA MELANOSTIGMA (Turner), comb. nov.

Fig. 8*G*; Plate 2, Fig. 3

Schoenobius melanostigmus Turner, 1922, Proc. Roy. Soc. Vict. **35**: 47.

Types.—The species was probably based on three females, not males as stated by Turner, collected by J. A. Kershaw. The holotype and one paratype, labelled "Claudie R., 1914, J. A. K." are in the National Museum of Victoria, Melbourne, and a paratype labelled "Claudie R., Queensland, 20-2-14, Nat. Mus. Victoria" is in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Paratype female.—Head, antenna, and palpi white; labial palpus with slight pale ochreous suffusion on outer surface, scales expanded, length of labial palpus four times diameter of eye. Thorax white, scales largely denuded; legs white, anterior and middle legs suffused with pale fuscous. Abdomen white. Forewing and cilia very pale ochreous white, a distinct dark fuscous semicircular blotch on lower distal extremity of cell, covering bases of veins M_2, M_3, and Cu_1; R_1 anastomosing with Sc; underside white. Hindwing and cilia white; underside white; frenulum a single stout bristle. Expanse 22·1 mm.

Female genitalia (paratype).—Ostium with some ill-defined sclerotization towards junction of ductus seminalis; apophyses short.

Distribution.—Known only from the original type specimens from the Claudie R., Cape York Peninsula, Qld.

Comments.—The genitalia of only the female paratype in the Division of Entomology Museum, C.S.I.R.O., have been available for study. The holotype, which is probably also a female, has had the abdomen of another insect glued to it. The absence of an anal tuft of long deciduous hair-scales in this abdomen, together with the genitalia, show that it does not even belong to the *Scirpophaga* group of genera. The second paratype, probably also a female, is without abdomen. The frenulum in this species, being a single stout bristle as in the male, does not indicate sex.

The species is only tentatively assigned to *Tryporyza*, for the male is unknown and further female specimens need to be studied. Several characters exhibited by the three type specimens are not in agreement with the generic description, but until further specimens are available, it would be unwise to broaden the generic description to accommodate it. The labial palpi, for example, are much longer than in the other species referred to *Tryporyza* and the scales are strongly expanded. In addition, R_1 of the forewing anastomoses with Sc, a character not known in the other species of *Tryporyza*. Again, in the females of both *T. innotata* and *T. incertulas*, the frenulum is a pair of closely appressed bristles instead of a single bristle as in *T. melanostigma*. All these characters are suggestive of *Niphadoses* rather than *Tryporyza*. However, the very broad ostium and the general form of the female genitalia in the paratype are suggestive of *Tryporyza*, although some indeterminate sclerotization within the ostium is present.

Genus TIPANAEA Walker

Tipanaea Walker, 1863, List Lep. Ins. Coll. Brit. Mus. **28**: 522.

Type species *Tipanaea patulella* Walker. This is the first species originally included by Walker in the genus. There appears to be no previous citation.

Proboscis short, weak; antenna in male finely serrate and ciliate, in female shorter, with short cilia; labial palpus (Fig. 2*F*) short in both sexes, ascending obliquely, smooth-scaled; apical segment about half length of second, slightly tapering, porrected; maxillary palpi with expanded scales, about two-thirds length of labial palpi. Forewing (Fig. 1*B*) broad, R_1 from two-thirds cell, closely approximated to Sc towards middle, R_2 from near upper angle of cell, R_3 and R_4 stalked from upper angle, R_4 to apex, R_5 near upper angle, closer to R_{3+4} than to M_1, M_1 from above middle, M_2 and M_3 approximated at base, M_3 from lower angle of cell, Cu_1 from well before angle, Cu_2 from two-thirds cell. Hindwing (Fig. 1*B*) with Rs and M_1 connate from upper angle of cell, Rs anastomosing with $Sc+R_1$ for a quarter of its length, M_2 and M_3 approximated at base, M_3 from lower angle of cell, Cu_1 from near angle, Cu_2 from just beyond half cell. Abdomen of male without brush of scales on posterior margin of seventh sternite, and without rounded membranous area on eighth segment; abdomen of female with a large and dense posterior tuft of deciduous hair-scales.

Male genitalia.—Uncus tapering to rounded apex; gnathos arms united in centre and drawn out abruptly to a slender tapering point, almost as long as uncus; tegumen with a dorsal Y-shaped thickening, the stem as long as the arms, a pair of small rounded membranous processes beneath at junction of tegumen and costa of valva; valva simple, quadrate, distal margin slightly convex: anellus membranous, finely spined, surrounding aedoeagus; aedoeagus nearly straight, cornuti represented by a row of short spines.

Female genitalia.—Ostium simple, membranous, cup-shaped, lined with scattered minute spines; ductus bursae short, broad, slightly sclerotized between entrance to ductus seminalis and ostium, with scattered minute spines; corpus bursae oval, membranous, without signum but with a few scattered minute spines near entrance to ductus bursae.

Only the type species of the genus *Tipanaea* is known. The genus can be readily distinguished from the other Australian genera by the very short labial palpi and the form of the genitalia in both sexes. Of diagnostic importance are the very small membranous subteguminal processes in the male.

TIPANAEA PATULELLA Walker

Figs. 1*B*, 2*F*, 3*I*, 3*J*, 8*H*; Plate 2, Figs. 8 and 9

Tipanaea patulella Walker, 1863, List Lep. Coll. Brit. Mus. **28**: 522.

Scirpophaga exsanguis Meyrick, 1882, Proc. Linn. Soc. N.S.W. **7**: 161 (type locality: Sydney or Brisbane; type lost).

Types.—Walker's description was based originally on five specimens, stated to be all males, one of which came from Moreton Bay, three from Sydney, and one from Australia without further data. Mr. D. S. Fletcher states (personal communication) that three of these specimens are still in the British Museum (Natural History) and he has selected a male labelled "58-124, Australia", which is hereby designated the lectotype (genitalia slide No. Pyralidae 5029).

Genitalia.—See under generic description.

Expanse.—Male 14·5–36·1 mm, female 17·9–40·0 mm.

Specimens examined.—52 ♂♂, 65 ♀♀.

Distribution.—Specimens have been examined by the author from coastal and subcoastal areas in eastern Australia from central Queensland to Victoria, and from Tasmania. In an unpublished catalogue, A. J. Turner also recorded the species from Thursday I. QUEENSLAND: Brisbane, Crow's Nest, Duaringa, Eumundi, Goodna, Gympie, Hedlow Creek (near Yeppoon), Rockhampton, Springbrook, Stradbroke I., Warra. NEW SOUTH WALES: Bateman's Bay, Brunswick Heads, Coraki, Ebor, Niagara Park, Sydney, Tabulum, Upper Allyn R., Wyangala Reservoir. AUSTRALIAN CAPITAL TERRITORY: Canberra. VICTORIA: Moe. TASMANIA: Launceston, Russell Falls, Scottsdale, Strahan.

Comments.—The great variation in size of this species seems to be roughly correlated with geographical distribution. The smaller specimens come largely from coastal New South Wales and from Queensland, and the larger specimens from the tablelands of New South Wales, from Victoria, and from Tasmania. Some of the largest specimens examined by the author, from Tasmania, southern Victoria, and Ebor, N.S.W., have the dorsum of the metathorax and the basal segment of the abdomen dark fuscous. These characters appear to be correlated with very slight differences in the male genitalia, which may be of subspecific significance. However, further specimens are necessary from those areas before firm conclusions can be drawn.

The frenulum in the female is a single stout bristle.

The species is common in swampy areas where *Juncus* (Juncaceae) occurs, and rushes of this genus will probably prove to be the larval host. Near Gympie, Qld., adults were taken resting during the daytime on stems of *Juncus* sp. and egg masses, covered with whitish scales matching those of the anal tuft of *T. patulella* females, were also present on these plants.

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Explanation of Plates 1 and 2

Plate 1

Fig. 1.—*Scirpophaga chrysorrhoa* Zell., male, Darwin, N.T.

Fig. 2.—*S. chrysorrhoa* Zell., female, Burringbar, N.S.W.

Fig. 3.—*S. xantharrenes*, sp. nov., holotype male, 12 miles E. of Duaringa, Qld.

Fig. 4.—*S. xantharrenes*, sp. nov., allotype female, 12 miles E. of Duaringa, Qld.

Fig. 5.—*S. limnochares*, sp. nov., holotype male, Coraki, N.S.W.

Fig. 6.—*S. limnochares*, sp. nov., allotype female, Coraki, N.S.W.

Fig. 7.—*S. imparella* (Meyr.), male, Colo R., N.S.W.

Fig. 8.—*S. imparella* (Meyr.), female, Bateman's Bay, N.S.W.

Fig. 9.—*S. helodes*, sp. nov., holotype male, Dingo, Qld.

Fig. 10.—*S. helodes*, sp. nov., allotype female, 12 miles E. of Duaringa, Qld.

Fig. 11.—*S. percna*, sp. nov., holotype male, Darwin, N.T.

Fig. 12.—*Helonastes acentrus*, sp. nov., holotype male, Dingo, Qld.

Fig. 13.—*H. acentrus*, sp. nov., allotype female, Dingo, Qld.

Plate 2

Fig. 1.—*Scirpophaga phaedima*, sp. nov., holotype male, Darwin, N.T.

Fig. 2.—*S. ochroleuca* Meyr., female, 25 miles N. of Gin Gin, Qld.

Fig. 3.—*Tryporyza melanostigma* (Turn.), paratype female, Claudie R., Qld.

Fig. 4.—*Catagela adoceta*, sp. nov., holotype male, 25 miles N. of Gin Gin., Qld.

Fig. 5.—*C. adoceta*, sp. nov., allotype female, 25 miles N. of Gin Gin, Qld.

Fig. 6.—*Tryporyza innotata* (Walk.), male, Ivanhoe, north-western Australia.

Fig. 7.—*T. innotata* (Walk.), female, Ivanhoe, north-western Australia.

Fig. 8.—*Tipanaea patulella* Walk., male, 18 miles S. of Gympie, Qld.

Fig. 9.—*T. patulella* Walk., female, 18 miles S. of Gympie, Qld.

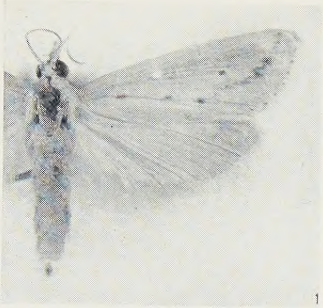
Fig. 10.—*Niphadoses palleucus*, sp. nov., holotype male, 25 miles N. of Gin Gin, Qld.

Fig. 11.—*N. palleucus*, sp. nov., allotype female, 25 miles N. of Gin Gin, Qld.

Fig. 12.—*N. elachia*, sp. nov., holotype female, Hedlow Creek, near Yeppoon, Qld.

Fig. 13.—*N. hoplites*, sp. nov., holotype male, 25 miles N. of Gin Gin, Qld.

Fig. 14.—*N. hoplites*, sp. nov., allotype female, 25 miles N. of Gin Gin, Qld.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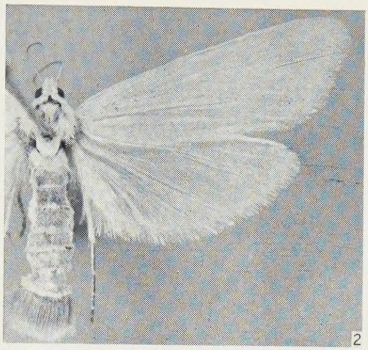
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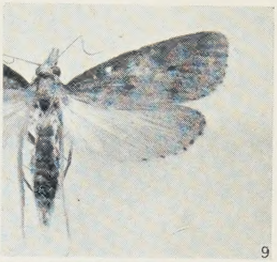
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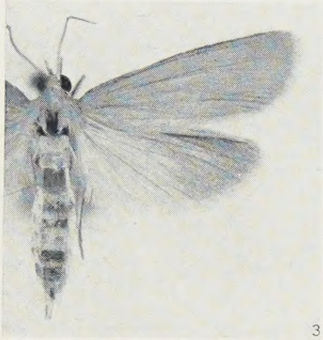
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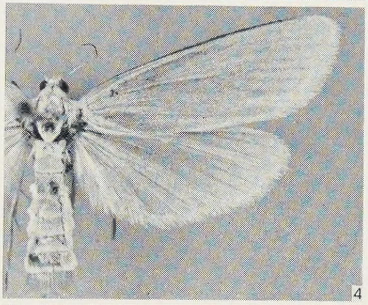
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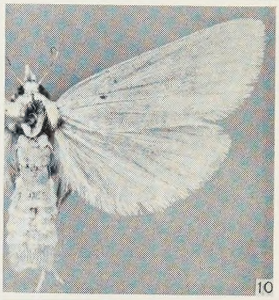
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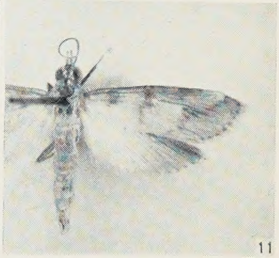
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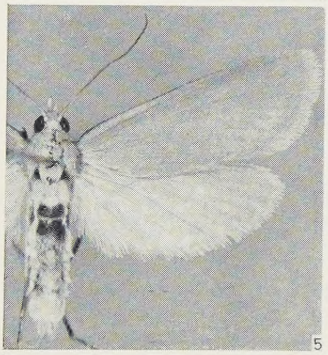
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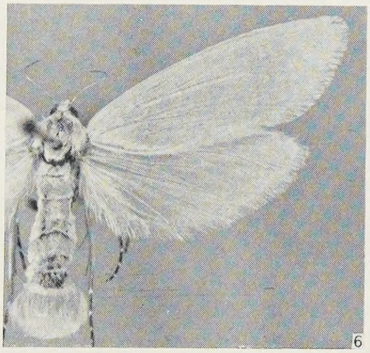
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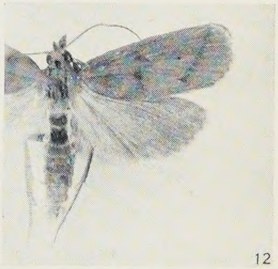
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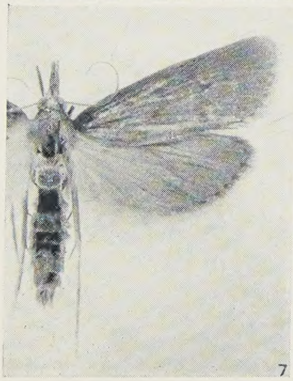
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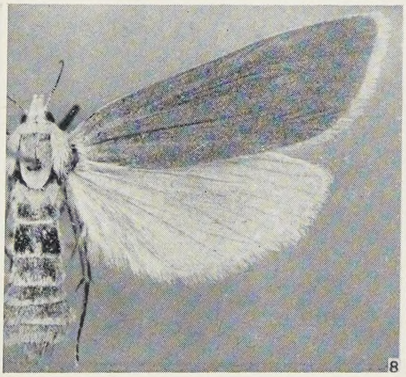
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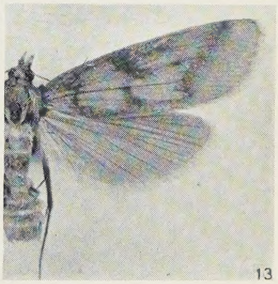
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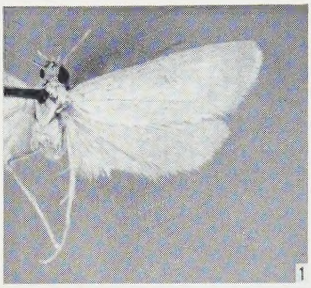
REVISION OF THE AUSTRALIAN STEM BORERS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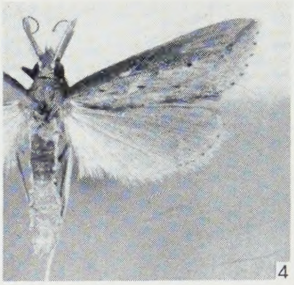
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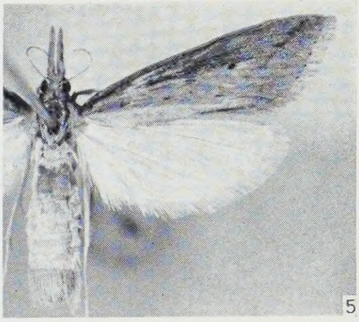
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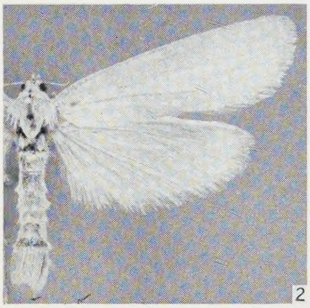
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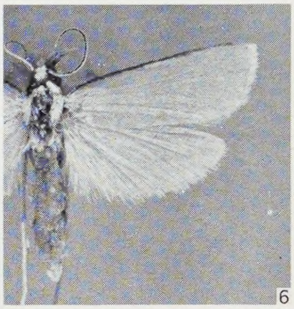
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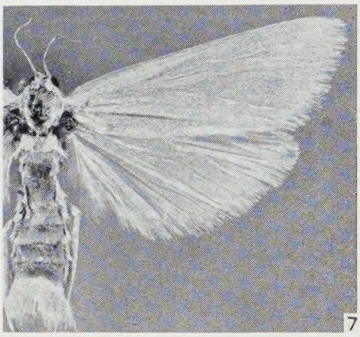
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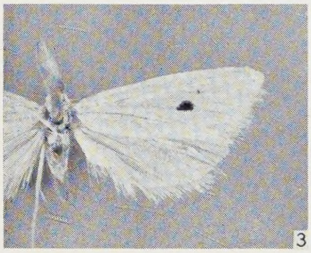
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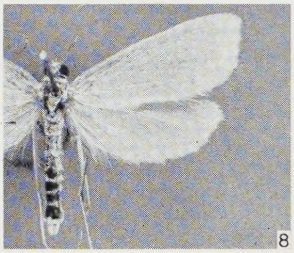
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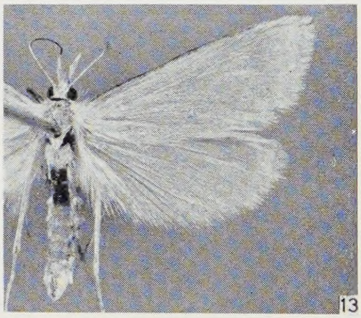
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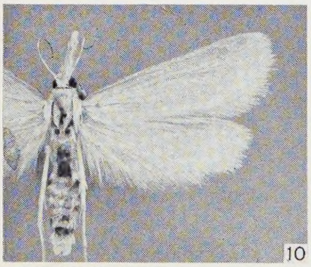
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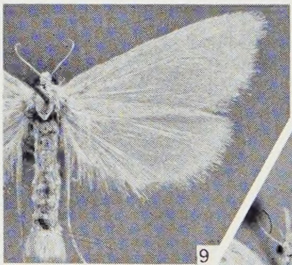
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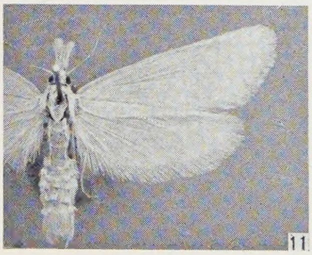
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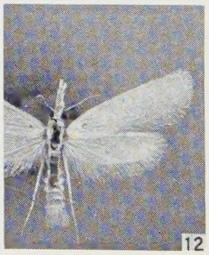
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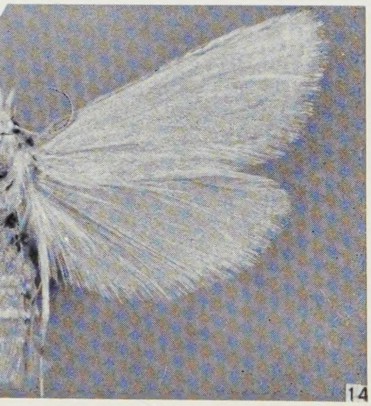
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